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Population ecology of the rusty parrotfish Scarus ferrugineus, a dominant grazer on a seasonal coral reef

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Population ecology of the rusty parrotfish *Scarus ferrugineus*, a dominant grazer on a seasonal coral reef

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NWO
Netherlands Organisation for Scientific Research

The research reported in this thesis was carried out at the department of Marine Biology which was part of the Center for Ecological and Evolutionary Studies (CEES) of the University of Groningen, the Netherlands. The project was financially supported by the Netherlands Foundation for the Advancement of Tropical Research (WOTRO grant W84-589) of the Netherlands Organisation for Scientific Research (NWO). The research was conducted in Eritrea using the laboratory and field facilities of the Marine Sciences Department of the former University of Asmara (UoA) and of the College of Marine Sciences and Technology of Massawa (COMSAT). Printing cost of this thesis was shared by the University of Groningen and the Faculty of Mathematics and Natural Sciences.

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Massawa was once called the pearl of the Red Sea. The city still retains its charm, although most of its iconic ottoman style architecture is now in ruins. It is said that if you visit Massawa you cannot help but fall in love especially if you have tasted its delicious fish. For me the main reason for falling in love with the city is the communal life and friendliness of the people of Massawa. My stay in this city, was one of the most joyous periods of my life (so far). All this was because of the lovely and hospitable people I met with. In this regard I would like to thank my friends Kibrom Tekeste and his lovely wife Yodit, Israel Amleke, Yohannes Teklemariam, Zahra, Suad, Ekram, Salah, Amanuel, Hamid Targella, Abu Hilal, Mitslal, Yodit, Demekesh.

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Yohannes Afeworki (ዮሃንስ አፈወርቂ)

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Chapter 1

General Introduction

The coral reefs of the southern Red Sea are among the most extreme habitats owing to their seasonality and extremely high summer temperatures. This thesis utilizes these characteristics to examine how grazers respond to changing conditions in the environment. The feeding behaviour, food intake, growth and reproduction of the parrotfish *Scarus ferrugineus* – a dominant grazer – are investigated in detail. The work summarizes field work conducted at Sheikh Said Island, Massawa Eritrea between 2005 and 2008. The findings are discussed with respect to the seasonally changing food resources and temperature. The first section of this chapter introduces coral reef ecosystems. This is followed by a brief description of what makes the southern Red Sea an extreme coral reef habitat and how the unusual environmental conditions prevailing here can be valuable for biological research. An account of parrotfishes as important members of the grazing guild on coral reefs and a brief description of the study species follow. An outline of the thesis wraps up this chapter.

1.1 Coral reef ecosystems

Coral reefs are tropical marine shallow water ecosystems restricted to 20 degrees North and South; these latitudinal limits are approximately corresponding to the oceanic winter isoclines of 18°C (Kleypas et al. 1999a). Coral reefs only cover about 0.2% of the ocean surface area (Spalding & Grenfell 1997; Vecsei 2004). Despite their marginal areal representation, coral reefs make a substantial contribution to overall ocean production because of their high primary productivity (Hatcher 1988; Crossland et al. 1991). It is estimated that coral reefs harbour about one third of all marine species, which makes them major repositories of global biodiversity (Reaka-Kudla 1997). Coral reefs are an important component of the global carbon cycle due to the large quantities of carbonate deposited within reefs; estimated at about 11% of the total marine production (Kinsey & Hopley 1991; Langer et al. 1997).

Coral reefs have offered a main source of protein for coastal human settlements since prehistoric times (Walter et al. 2000; Hardt 2009; Jones 2009). They still continue to provide a range of goods and services to humanity including fisheries, tourism, coastal protection, nutrient cycling and biological diversity (Moberg & Folke 1999; Cesar & van Beukering 2004; Barbier et al. 2010). One estimate places the global revenue generated from coral reefs around 30 billion US dollars per year (Cesar et al. 2003). For the economies of developing countries – where many coral reefs are located – the revenue generated from coral reefs is a substantial component of the Gross Domestic Product (GDP) (Burke et al. 2011).

Due to this long history of interaction with coral reefs, humans have contributed directly or indirectly to their degradation (Pandolfi et al. 2003; Mora 2008). Declining fish populations, reduced maximum sizes of exploited species and altered community structure of reefs have already been recorded from prehistoric times (Wing & Wing 2001; Fitzpatrick & Donaldson 2007; Hardt 2009; McClanahan & Omukoto 2011). Historical overfishing may have driven large predators to the point of being functionally extinct (Jackson et al. 2001; Pandolfi et al. 2003). At the present time, reef degradation has intensified further due to human population growth and technological advances (Cesar et al. 2003).

According to an opinion poll of coral reef researchers conducted in 2004, the primary causes of coral reef decline are overfishing, ocean acidification, coral bleaching from increased temperatures, sedimentation and nutrient enrichment (Kleypas & Eakin 2007). Globally, the sea surface temperature (SST) has risen by 0.59°C over the last 135 years (Roemmich et al. 2012). The increasing frequency and severity of temperature anomalies and associated coral bleaching events in recent years have made warming the top threat for coral reefs (Glynn 1993; Hoegh-Guldberg 1999; Wilkinson 2004; Halpern et al. 2008). Currently global temperatures are predicted to rise (Solomon et al. 2007) and the rate of increase appears to be faster for enclosed seas such as the Red Sea and the Mediterranean (Sherman et al. 2009; Raitsos et al. 2011). It is expected that tropical coral reefs will see an unprecedented decline owing to increasing frequency of bleaching events (Hoegh-Guldberg 1999; Donner et al. 2005; Hoegh-Guldberg et al. 2007) and reduced calcification rates (Hoegh-Guldberg et al. 2007; Kleypas & Yates 2009; Veron et al. 2009). Current estimates indicate that up to 19% of the reefs are considered highly degraded (Wilkinson 2008). If all present day threats to coral reefs remain as they are, an additional 15% are predicted to join this category by 2030 (Wilkinson 2008).

Following mass mortality events, live coral cover and coral species diversity decline sharply and the exposed area is quickly covered by thick turfs or invertebrates (Hoegh-Guldberg 1999; McClanahan et al. 2001; Aronson et al. 2002; Diaz-Pulido & McCook 2002; Norstrom et al. 2009). Turfs may develop into stands of erect macroalgae under suitable conditions, such as the absence of grazers (Hughes 1994; Done 1999; Hughes et al. 2007; Bruno et al. 2009). Coral reefs that have thus been altered, typically take 1 – 2 decades to recover coral cover to a level that existed before the catastrophe (Connell 1997; Sano 2000; Adjeroud et al. 2009; Graham et al. 2011). Some of the factors that affect the likelihood of recovery are the nature of the disturbance (chronic vs. acute) (Connell 1997), connectivity or the degree of isolation of the reef (Halford & Caley 2009), and the geographic location (Connell 1997; Graham et al. 2011). The regional differences in recovery rates: such as the higher likelihood of recovery of Indo-Pacific reefs compared to western Atlantic reefs (Connell 1997) or the faster recovery of reefs from the western Pacific compared to the more isolated eastern Pacific (Graham et al. 2011) is partly attributed to the poorer species diversity and lower functional redundancy of these reefs (Bellwood et al. 2004; Graham et al. 2011). Generally, reefs with a diverse and abundant grazer community appear to recover faster than those whose grazer communities are impoverished e.g. by overfishing (Hughes et al. 2007; Sheppard et al. 2008; Halford & Caley 2009; Houk et al. 2010; Adam et al. 2011).

Grazers promote the recovery of coral reefs by reducing the cover of fleshy and canopy forming algae and increasing the cover of crustose corallines – both these conditions favour the recruitment and growth of corals (Sammarco 1982; Mumby et al. 2007; Mumby & Harborne 2010). The effectiveness of grazers in reducing algal cover is best illustrated by the tendency for algal cover to be low in protected compared to fished reefs (Williams & Polunin

2001; McClanahan & Graham 2005; Stockwell et al. 2009; Wismer et al. 2009). In addition, controlled experiments of herbivore exclusion (caging) conducted in conjunction with nutrient enrichment have largely confirmed the preponderant role of grazers over nutrient loads in controlling benthic algae (McCook 1999; Szmant 2002; Heck & Valentine 2007; Burkepile & Hay 2009). It is now widely accepted that grazers are a key component of the resilience capacity of coral reefs and that their conservation is of primary importance in the management of coral reef ecosystems (Hughes et al. 2003b; Bellwood et al. 2004; Hughes et al. 2007; Nystrom et al. 2008).

Box 1.1 The role of grazing in resilience of coral reefs to phase shifts

Ecological communities are distinguishable by the relative abundances of the species that compose them. Different environmental conditions support distinct assemblages of species that we call communities or ecosystems. For example, tropical coral reefs thrive in shallow water with plenty of light where temperatures and aragonite concentration do not drop or rise beyond critical values (Kleypas et al. 1999a). When environmental conditions change the relative composition of the species may change leading to a different assemblage of species. Chronic and gradual changes in environmental parameters are referred to as "press" events; whereas acute and short-term disturbances are called "pulse" events (Bender et al. 1984; Connell 1997).

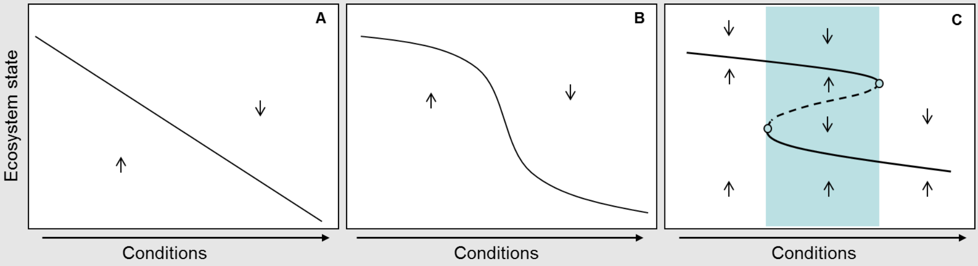

Fig. B1.1.1 Behaviour of ecological communities under changing conditions such as anthropogenic stressors. (A) An ecosystem changing its state (assemblage of species) gradually. (B) A phase shift in which an ecosystem plummets into a different community within a narrow band of change in conditions. (C) Multiple stable states in an ecosystem (shaded area). Solid lines are stable equilibrium and broken line is unstable equilibrium. Open circles are bifurcation points (adapted from Scheffer et al. (2001)).

Ecosystems may respond to changing conditions through a gradual shift in species assemblages as is shown in (Fig. B1.1A) (Spencer et al. 2012). When the change in the ecosystem state is gradual, the removal of the disturbance should likely lead to restoration of the system to its former state. However there are numerous examples where, within a narrow range of change in conditions, ecosystems have precipitously shifted to a different species assemblage (Fig. B1.1B) (Scheffer et al. 2001; Folke et al. 2004). This sort of change has been called phase shift in ecological terminology (Dudgeon et al. 2010). Ecological theory however predicts a third kind of response where alternative stable states (ASS) can exist under similar environmental conditions (Fig. B1.1C) (May 1977; Connell & Sousa 1983; Dudgeon et al. 2010). Recent models of coral reefs suggest that for certain values of grazing intensity and nutrient concentrations, coral reefs can exist as algae dominated or coral dominated alternative states (Mumby 2009; Fung et al. 2011).

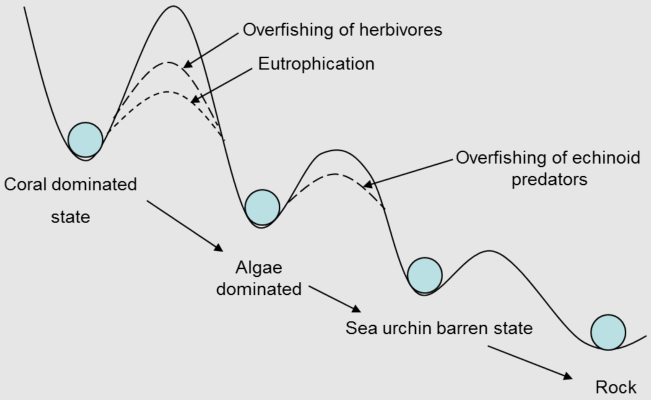

Fig. B1.1.2 Schematic representation of phase shifts and changing resilience under anthropogenic stress in coral reef ecosystems. Overfishing and nutrient pollution flatten the landscape weakening the resilience of the system. Coral-algae phase shift is the most frequently observed event. Nevertheless under increased human disturbances reefs can further degrade into sea urchin barrens and finally in to slime (adapted from Bellwood et al. (2004)).

It is still being debated whether the recent catastrophic changes in coral reefs constitute phase shifts or cases of ASS (Mumby 2009; Dudgeon et al. 2010; Fung et al. 2011). Recent analysis of large scale benthic cover data of coral reefs strongly suggests that ASS do not exist (Bruno et al. 2009; Zychaluk et al. 2012). Most of the recent changes in coral reefs occurred in altered environments following a prolonged human impact including increases in nutrients, sedimentation and overfishing (Jackson et al. 2001; Pandolfi et al. 2003; Mora 2008). In this regard the switch to the algae dominated state appears to be a result of changed environmental and state parameters; hence these changes are likely to be phase shifts (Connell & Sousa 1983; Dudgeon et al. 2010; Zychaluk et al. 2012). In accordance with the phase shift scenario, degraded reefs did show recovery of the corals where grazers have been recovered or where nutrient enrichment has been reduced (Maragos et al. 1985; Edmunds & Carpenter 2001; Carpenter & Edmunds 2006; Idjadi et al. 2006). The observation that reefs impacted by chronic disturbances are less likely to recover compared to those impacted by pulse events further supports a phase shift explanation (Connell 1997). Many of the state changes in coral reefs are therefore more likely to be cases of phase shift than of alternative stable states (Petraitis & Dudgeon 2004; Dudgeon et al. 2010).

The concept of ecological resilience is an integral part of phase shifts – it refers to the amount of disturbance a system can withstand before it changes into a different state (Holling 1973; Gunderson 2000). Ecological resilience has been traditionally represented by the cup-and-valley diagram (Fig. B1.1.2) (Gunderson 2000). The valleys (cups) represent basins of attraction into which the community gravitates after a disturbance. Disturbances have to be either persistent or strong enough to nudge the ball out of one cup into another. This represents a phase shift. In this scheme the height of the cup and its width represent the resilience of the system (Gunderson 2000; Bellwood et al. 2004). Changes in the environmental parameters that tend to flatten the landscape will weaken the resilience of the system (Bellwood et al. 2004; Dudgeon et al. 2010). Reduced herbivory and eutrophication are two of the primary factors that impinge on the resilience of coral reefs (Lapointe 1997; Szmant 2002; Hughes et al. 2003b; 2003a; McManus & Polsenberg 2004; Nystrom et al. 2008). The relative importance of these two is debated among coral reef scientists (McCook 1999). Nevertheless an increasing number of experimental and field studies are revealing that herbivory, rather than nutrient enrichment plays a predominant role in controlling algal biomass in coral reefs (McCook 1999; Burkepile & Hay 2006; Heck & Valentine 2007; Furman & Heck 2008). Grazers such as parrotfishes are clearly critical for reef resilience and their removal by overfishing will make coral reefs increasingly vulnerable to phase shifts.

Because of their crucial role, herbivores have become one of the focal points of coral reef research (Mumby & Steneck 2008). One aspect that is in urgent need to be investigated is how coral reef fish populations will be affected by rising temperatures (Wilson et al. 2010). The effects of high temperature on reef fishes have only being investigated recently (Mora & Ospina 2001; Munday et al. 2008; Donelson et al. 2011). Possible effects that need to be investigated are whether community structure and abundance of grazers will change, how their demography will be altered and finally whether the impact of grazers on the benthos will be affected (Wilson et al. 2010). One way to approach these questions is by investigating processes in extreme environments, such as the Persian Gulf and the southern Red Sea (Ateweberhan et al. 2006a; Feary et al. 2010; Afeworki et al. 2011). The work reported in this thesis studies an important grazer population on a southern Red Sea coral reef, which is known for its high levels of seasonality in algal cover and extremely high summer temperatures. By studying feeding, growth and reproduction of that dominant grazer, we hope to provide clues as to how grazers in general will respond to changing benthic communities and to warming seas elsewhere.

1.2 The southern Red Sea: an extreme coral reef environment

The southern Red Sea is bordered in the east by Yemen and in the west by Eritrea. This area is characterized by a wide and shallow continental shelf (Braithwaite 1987). As a consequence, there is high potential for nutrient exchange between the shallow bottom and the water column, making this area relatively nutrient rich. In addition this part of the Red Sea receives year round input of nutrient rich water from major upwelling zones in the NE Indian Ocean. These factors combined make the southern Red Sea more productive, compared to the central and northern parts (van Couwelaar 1997; Veldhuis et al. 1997, Fig. 1.1). These oceanographic conditions are thought to contribute to the limited coral reef formation in this area (Roberts et al. 1992).

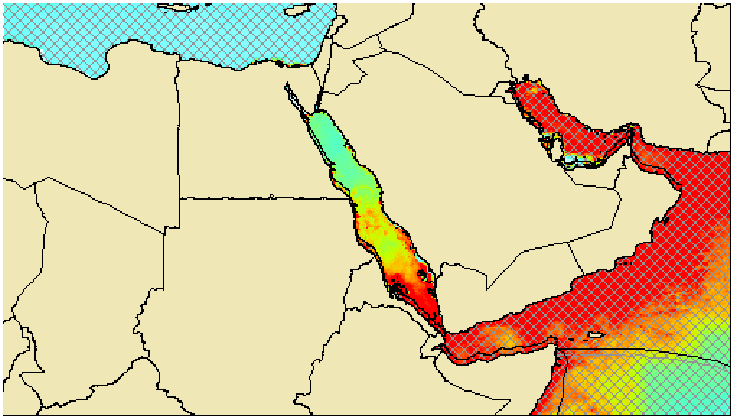

Fig. 1.1 Mean annual primary production (mg C m^{-2} day^{-1}) of the Red Sea and the Arabian Sea. Figure taken from the sea around us project of the University of British Columbia (www.seaaroundus.org).

SSTs of the southern Red Sea are among the highest recorded for coral reefs (Ateweberhan et al. 2005a; Ateweberhan et al. 2006a). Maps of Red Sea SST clearly show that the southern Red Sea is the hottest region, particularly the coastal area around Massawa (Edwards 1987). Mean monthly SST derived from*in situ* hourly records at 2 m depth from Massawa exceed 32°C for four to six months of the year depending on reef location and exposure (Ateweberhan et al. 2006a). Maximum temperatures at the peak of summer reach 34 – 35°C. These values are extreme when compared to other reef sites (see Fig. 1.2); especially considering that coral bleaching elsewhere usually takes place when temperatures exceed 30 – 31°C for a few weeks (Hoegh-Guldberg 1999; McClanahan et al. 2001; Aronson et al. 2002; Berkelmans 2002).

Temperature is a key environmental parameter that affects all aspects of the biology of a species from its physiology to its distributional range. For corals temperature plays a key role, among the many factors that limit their distribution, such as light, calcium carbonate concentration and salinity (Hoegh-Guldberg 1999; Kleypas et al. 1999a). Kleypas et al. (1999a) analysed global distribution of coral reefs and showed that marginal coral reef habitats – areas where reef development is poor – are associated with both low and high temperatures. The "high-temperature" marginal habitats appear to be restricted to enclosed tropical seas such as the Red Sea and the Persian Gulf.

The other major environmental parameter that is associated with coral reef formation is the saturation state of aragonite (Ω_{ar}), the calcium carbonate mineral precipitated by reef building corals (Kleypas et al. 1999a; Veron et al. 2009). Increased CO2 in sea water lowers the pH

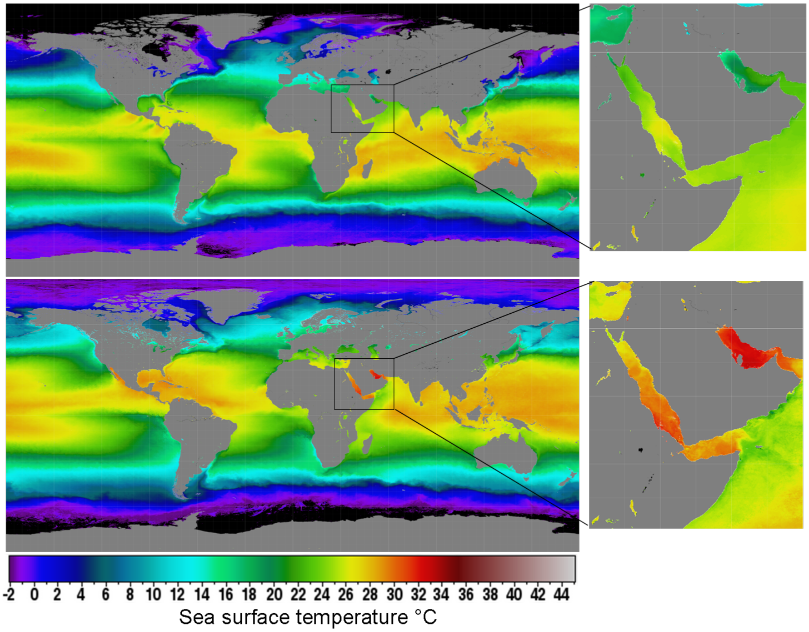

Fig. 1.2 Mean sea surface temperature (SST) for January (top) and September (bottom) averaged over the years 2002 –2012. Insets show close ups of the trend within the Red Sea and the Arabian Sea. Extreme summer temperatures of southern Red Sea and Arabian Gulf stand in stark contrast to the milder temperatures elsewhere in the tropics. The effect of the summer upwelling is clearly depicted in the lowered SST in the Arabian Sea and the Gulf of Aden. SST measured by MODIS/AQUA satellite (source: http://oceancolor.gsfc.nasa.gov/).

leading to a lower Ω_{ar} (Kleypas et al. 1999b). Since the dissolution of CO2 in seawater is inversely related to temperature, hot areas such as the southern Red Sea tend to have high pH and consequently have one of the highest Ω_{ar}. This area is thus not immediately threatened by ocean acidification (Kleypas et al. 1999a). Salinity values in the Red Sea increase from near oceanic values of 36.5 parts per thousand (ppt) in the South to 42 ppt in the North (Morcos 1970). Average salinity in the southern Red Sea is 36.5 ppt (Turak et al. 2007), a value well within the tolerance range of corals (Coles 2003). In summary it appears that the extreme summer temperature is perhaps the primary structuring force of the southern Red Sea coral reefs.

The harsh environmental conditions in the enclosed Persian Gulf and the Gulf of Oman, have resulted in species poor coral and fish communities (Coles & Tarr 1990; Riegl 1999; Coles 2003; Feary et al. 2010; Burt et al. 2011). Likewise the coral reefs of the southern Red Sea have been generally considered poorly developed with fewer species of fish as well as corals compared to their northern counterparts (Roberts et al. 1992; Sheppard et al. 1992; Righton et al. 1996). However, marine biodiversity of the southern Red Sea is not as impoverished as it was previously thought. Recent works in the area have invariably resulted in considerable increases in species counts for soft corals (Benayahu et al. 2002), hard corals (Turak et al. 2007), and fishes (Zekeria et al. 2005). This suggests that the paucity of sampling in this area is partly responsible for the reports of low diversity. Compared to the Persian Gulf, the relatively mild conditions of the southern Red Sea may render it less inhospitable. Moreover its geographic position – being the meeting point of the Red Sea and the Indian Ocean – increases the potential for higher species diversity.

Box 1.2 Zonation and seasonality of the coral reef algae of Sheikh Said Island

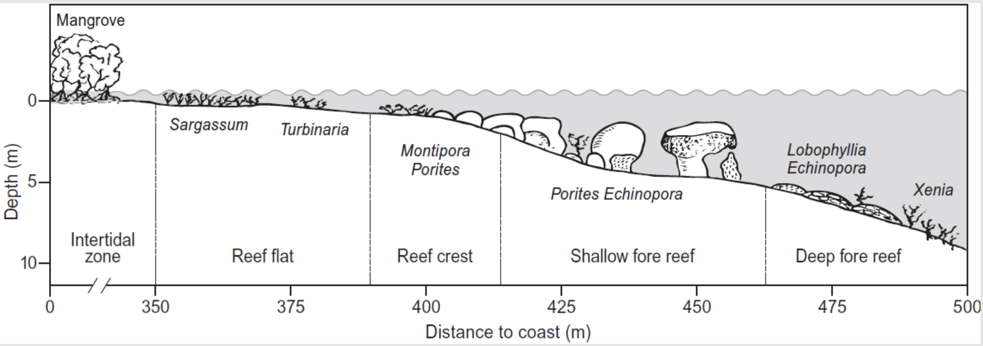

Fig. B1.2.1 Profile of the fringing reef of Sheikh Said Island and the zonation of dominant biota. Image by Dick Visser.

Macroalgal diversity and abundance are higher in the south than in the central and northern parts of the Red Sea (Lipkin & Silva 2002; Ateweberhan & van Reine 2005). This correlates with the larger extent of shallow area and relatively higher nutrient levels in this part of the Red Sea. In contrast coral reef development as well as fish and coral species diversity is lower in the south than in the north and central Red Sea.

The shores in the Eritrean Red Sea are primarily calcium carbonate platforms that were formed during the latter sea-level high stands of the Pleistocene (Hoang et al. 1996). These platforms support crustose coralline reefs, macroalgal bands and coral reefs. The shallow reef flats are dominated by macroalgae such as *Sargassum illicifolium* and *Turbinaria triquetra* (Ateweberhan 2004; 2006a; Fig. B1.2.1). The outer reef flat and the reef crest are dominated by crustose corallines and turf algae. The shallow and deeper parts of the fore reef are largely dominated by live corals, crustose corallines, turf algae and soft corals (Ateweberhan et al. 2006a; Afeworki et al. 2011).

The southern Red Sea experiences considerable seasonal changes in photosynthetically available radiation (PAR), SST and wind speed and direction (Ateweberhan et al. 2006a).

These changes (particularly that of temperature) effect dramatic changes in the composition and biomass of different functional groups of algae (Fig. B1.2.2). Macroalgae, folios algae and crustose corallines dominate their respective zones in the cool season. Their growth and reproduction peaks during the cool part of the year.

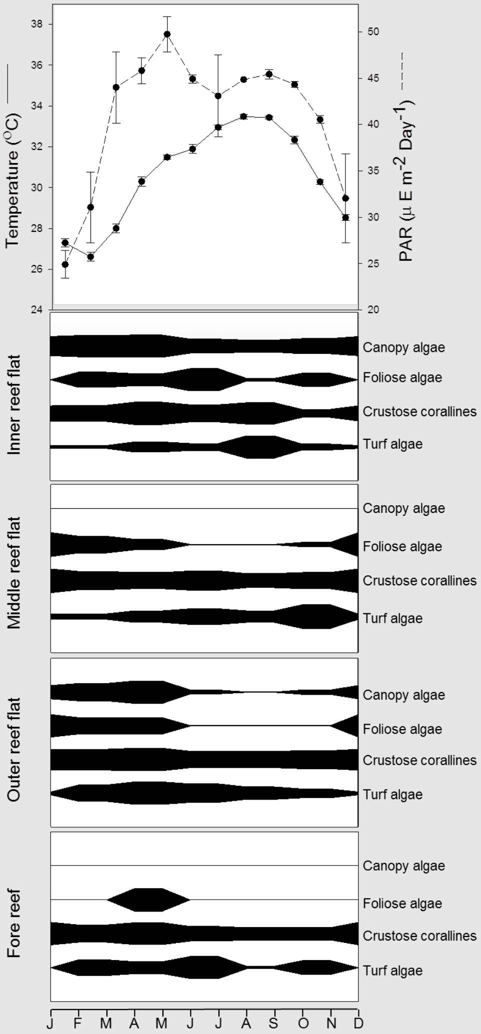

Fig. B1.2.2 Monthly water temperature, photosynthetically available radiation (PAR), and the phenology of four functional groups of coral reef algae at Sheikh Said Island in the southern Red Sea. Kite values are percentages relative to the maximum biomass of each functional group for each reef zone. Adapted from (Ateweberhan et al. 2006a).

With the onset of the hot season macroalgae and foliose algae stop growth and reproduction, loose their thallus, and survive the extreme summer temperatures (34 – 36°C) in their holdfast stage (Ateweberhan et al. 2005a,b, 2006b). Summer also witnesses the death of crustose corallines which are sloughed off leaving the space for turfs to occupy (Fig. B1.2.2). As a result turfs achieve the highest cover in the hot parts of the year (Ateweberhan et al. 2006a).

Southern Red Sea macroalgae are "season anticipators" a characteristic typical of high latitude macroalgae. Season anticipators are algae that initiate growth or primary laterals with stored resources well before the period of optimal growth. The optimum period for growth and reproduction in the southern Red Sea is narrow (4 months). To maximize growth and reproduction, algae start initiation of primary laterals in October/November when water temperatures are higher than that of April/May when the die off happens (Ateweberhan 2004). The initiation starts well before temperatures are optimal for growth and reproduction. The narrow optimum period also constrains the times in which reproduction and growth take place in these algae. Indeed in three species of brown algae studied, reproduction and growth overlap with no trade-off between them (Ateweberhan et al. 2005a; 2006b; 2008). These as well as the high amplitude biomass changes – macroalgae lose 70 – 99% of their biomass in summer – suggest that the southern Red Sea is a highly seasonal environment (Ateweberhan et al. 2005a, 2006a).

The annual water temperature in the southern Red Sea has a range of 10°C from 25 – 35°C (Ateweberhan et al. 2006a). This range is smaller than in many other reef areas (Coles & Fadlallah 1991). This limited range, however, is now known to drive a highly seasonal rhythm in growth and reproduction of reef organisms because the upper temperature is a limiting factor for many organisms (Guillaume et al. 2000; Ateweberhan et al. 2005, 2006b). The seasonality is further accentuated by other changes such as increased irradiance and inflow of the nutrient rich Indian Ocean water in summer (Ateweberhan et al. 2006a). During the cool months, cloud cover is high and irradiance low (see Box 1.2) and hence pelagic productivity tends to be lower (Fig. 1.1). In summer, high temperature and irradiance are detrimental to most of the benthic algae in shallow reef zones, with the exception of tolerant and hardy turfs. As a result there is a dramatic seasonal change in community structure of benthic algae (see Box 1.2). Seasonal change in primary producers is expected to propagate to other trophic levels. Seasonality is likely to be more pronounced in the lower trophic levels such as grazers compared to carnivores (Clarke 1988). In addition, the extreme summer temperatures can be expected to affect feeding rate and growth of reef fishes. Studies investigating these effects have only been made recently and they report significant seasonality in feeding, growth and reproduction (Zekeria 2003; Zekeria et al. 2006; Afeworki et al. 2011).

If global temperatures rise as predicted, habitat marginality in coral reef areas is likely to increase over time (Guinotte et al. 2003). This is particularly true for the Red Sea (see Box 1.3) and other regional seas which have experienced faster rises in SST than the global averages (Sherman et al. 2009; Raitsos et al. 2011). The southern Red Sea already has stressful conditions and a further increase in temperature is likely to make it inhospitable to many species. Since the effects of high temperature are species specific and size dependent (Mora &

Ospina 2001; Hernandez et al. 2002; Eme & Bennett 2009; Peck et al. 2009), its overall effect on marginal coral reefs such as the southern Red Sea will be further declines in species richness and alteration of community structure (Walther et al. 2002; Munday et al. 2008; Barneche et al. 2009; Wilson et al. 2010). This area is further threatened by development activities and by shipping density which is among the highest in the world (Halpern et al. 2008; Sheppard et al. 2010).

1.3 Parrotfish grazing on coral reefs

The fossil record shows that fish herbivory as a major force appeared in reefs during the Eocene (Bellwood 2003). Escalation in herbivory in the Cenozoic, in particular the evolution of an excavating feeding mode in the scarines is thought to have affected benthic communities profoundly, ushering the dominance of crustose corallines in modern reefs (Steneck 1983; Bellwood 2003). In present day coral reefs, herbivorous fishes compose a considerable proportion of the overall fish biomass (Ogden & Lobel 1978; Williams & Hatcher 1983). On many modern coral reefs parrotfishes are the biomass dominant grazers (Williams & Polunin 2001).

Parrotfishes belong to the scarines tribe of the family Labridae (Westneat & Alfaro 2005), comprising about 603 extant species of which 99 are parrotfishes (Parenti & Randall 2011). Evolutionary processes that led to the present day parrotfish diversity may have involved three major events. The first was the divergence from a sister Labrid group (the Cheilinini) about 50 million years ago (Cowman et al. 2009). The ancestor that split from the Cheilinini may have been a browser feeding of macrophytes (Bellwood 1994; Cowman et al. 2009). The second major event is the split of the group into the seagrass and reef dwelling clades (Bellwood 1994; Streelman et al. 2002; Cowman et al. 2009; Kazancioglu et al. 2009). This split was along feeding ecology lines and involved the evolution of a specialized feeding apparatus such as the fused teeth and modified oral jaws adapted to excavate and process algae growing on hard substrates that characterise coral reef habitats (Bellwood 1994; Streelman et al. 2002; Kazancioglu et al. 2009). The final major episode is the accelerated diversification of the reef clade, believed to have been driven by sexual selection associated with the territorial behaviour and sexual dichromatism that is characteristic of most parrotfishes (Streelman et al. 2002; Kazancioglu et al. 2009).

Parrotfishes scrape or excavate the substrate when feeding; impacting it more than any other grazing fish (Brock 1979; Steneck 1988; Bonaldo & Bellwood 2009; Bonaldo et al. 2011). The feeding scars leave a cleared area that is available for colonization by corals and other invertebrates (Bonaldo & Bellwood 2009; Bonaldo et al. 2011). Due to the powerful bites on the substrate, parrotfishes also play an important role in bioerosion, sediment reworking, and structuring of the habitat (Brock 1979; Hay 1981a; Bellwood 1995b; Bruggemann et al. 1996; Bellwood et al. 2003). The role of parrotfishes in reef throphodynamics may be high considering their fast growth (Russ & St.John 1988; van Rooij et al. 1995b) and high mortality due to predation (Sudekum et al. 1991; Clifton & Robertson 1993; DeMartini et al. 2005; 2008).

Box 1.3 Rapid warming of the Red Sea

Satellite records of sea surface temperature (SST) for the years 1982 – 2008 were extracted for a grid close to the study site from the coral reef temperature anomaly dataset (CoRTAD) derived from the AVHRR-based data records (NOAA). Hourly SST was recorded *in situ* from 2003 – 2006 using underwater loggers at 2 m depth on the study site. A comparison of *in situ* and satellite SST shows that the satellite data is lower than *in situ* measurements (Table B1.3.1). Other studies have reported comparable 'cool' bias in satellite SST estimates (Castillo & Lima 2010). The satellite SST was therefore corrected using the correction factors (Table B1.3.1).

Table B1.3.1 Summary of comparison of *in situ* and satellite estimated SST of Sheikh Said Island, Massawa, Eritrea.

Paired-comparisons	Mean difference (±SE)	*t*	*df*	*P*
In situ day time SST – Satellite SST	1.16 (±0.10)	12.07	83	0.00
In situ night SST – Satellite SST	0.82 (±0.11)	7.71	83	0.00
In situ day SST – *In situ* night SST	0.34 (±0.05)	6.38	83	0.00

Plot of the corrected long-term satellite SST, clearly shows a significant warming in the Red Sea in the mid 1990s (Fig. B1.3.1) and agrees with the findings of (Raitsos et al. 2011). The SST of the years beyond 2000 have remained at the level of those recorded in 1998 – a year in which coral reefs all over the world saw an unprecedented bleaching (Goreau et al. 2000). If global temperature rises as is predicted (Solomon et al. 2007), the warm phase in the Red Sea will be expected to persist. Such fast change in temperature is likely to limit the capacity of marine organisms to adapt (Hoegh-Guldberg et al. 2007). Significant reduction in growth of an important reef building coral species has already occurred since this warming started (Cantin et al. 2010). Similar negative effects are to be expected for fishes at the individual, population and community level.

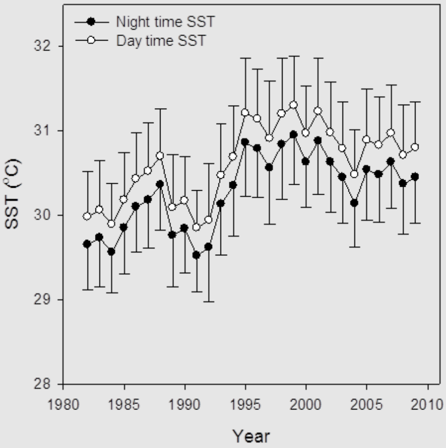

Fig. B1.3.1 Mean (±95% CI) of monthly sea surface temperature (SST) of Sheikh Said Island, Massawa, Eritrea.

1.3.1 *Scarus ferrugineus*: the rusty parrotfish

Scarus ferrugineus Forsskål 1775 is endemic to the Red Sea and the Arabian Sea (Randall & Ormond 1978) and is one of 18 parrotfish species in the Red Sea. About 11 of these have been recorded in the southern Red Sea. In the Red Sea, *S. ferrugineus* is one of the most common species and in the southern Red Sea it is the dominant grazer in terms of biomass (Afeworki et al. 2013). The fact that it was one of the first species to be described by Forsskål during the Danish Arabian expedition in 1762 (Randall & Ormond 1978) is testimony to its historical high abundance in the southern Red Sea.

Fig. 1.3 *Scarus ferrugineus*. Left: female (initial phase) foraging on dense turfs. Right: male (terminal phase) being attended to by the cleaner wrasse *Labroides dimidiatus*. Southern Red Sea, Eritrea (Photos by Y.A.).

S. ferrugineus is a medium sized parrotfish reaching a maximum length of 36 – 40 cm in the southern Red Sea depending on the location (Afeworki 2003). Like other labrids, *S. ferrugineus* is a diandric protogynous hermaphrodite (Abdel-Aziz et al. 2012, Chapter 7). The larger sized males (terminal phase, TP) and the smaller female (initial phase, IP) are distinctly coloured (Fig. 1.3). Males keep temporary spawning territories in the deeper sections of the reef where they compete for space and females. Its abundance, large body size and its tendency to be unaffected by the close presence of observers make this species an ideal candidate for detailed behavioural studies. In spite of these qualities, no prior studies on this important reef grazer have been undertaken.

1.4 Outline of the thesis

Chapter 2 describes how commonly occurring grazing fish species partition the habitat and examines whether habitat use varies temporally. Using underwater visual census techniques, abundance, and biomass and size structure of the common grazers is studied in four reef zones during four periods of the year. In addition, grazing pressure is quantified using caging experiments in three of these reef zones. The observed patterns in habitat use and grazing intensity are discussed in relation to food availability, temperature and predation.

Chapter 3 deals with food availability and selection by different life phases of *S. ferrugineus* during the hot and cool seasons. Benthic communities are described in detail using chain-link transects in three reef zones; the reef crest, the shallow fore reef zone and the deep fore reef. Bites from three life phases (juveniles, IP and TP) are described during the two seasons. The feeding preferences and seasonal changes in food preference are investigated. Food preference in relation to life phase and availability of resources is discussed.

Chapter 4 presents the seasonal changes in food intake rates, analysing the effect of size and life phase. Bite rates and bite sizes (g of food bite^{-1}) are determined from field observations during different seasons. Seasonality in intake rates and bite rates is discussed in relation to intrinsic factors such as territorial behaviour, body size, sex and extrinsic factors such as temperature and food availability.

Chapter 5 addresses the effect of seasonally changing food resources and intake rates on growth and condition of IP, TP and transitional (individuals changing sex) *S. ferrugineus*. Using tagging techniques, length increments have been recorded over various time spans. Growth is compared between seasons using ordinary ANCOVA. In addition growth is modelled using GROTAG. Seasonal change in growth is discussed in relation to varying resource levels and temperature, while differences in growth between the sexes are discussed in relation to life history decisions and sex change theory.

In **Chapter 6**, the demography and growth pattern of *S. ferrugineus* is investigated using age-length data derived from otolith annulus reading. Validated otolith annulus readings are used to determine the age of fish ranging in size from 5 – 36 cm fork length. Growth, longevity, and mortality rates are estimated for IP and TP fish. Differences in demography between males and females are discussed in relation to sex change theories and the extreme environment of the southern Red Sea.

Chapter 7 treats the seasonality in the reproduction of *S. ferrugineus* and its environmental and physiological correlates. This is studied using monthly samples of gonad index, histological sections of gonads and behavioural observations. Intra-annual variation in environmental parameters such as wind intensity and pelagic primary production is presented. Physiological condition of individuals is assessed using liver, and body weight indices. The timing of reproduction is discussed in relation to the timing of growth and the dynamics of body reserves. **Chapter 8** describes the sexual patterns and mating tactics of *S. ferrugineus* based on histological examination of gonads and behavioural observations. A general discussion and a summary of the main findings of the thesis is provided in **Chapter 9**.

CHAPTER 2

SEASONALLY CHANGING HABITAT USE PATTERNS AMONG ROVING HERBIVOROUS FISHES IN THE SOUTHERN RED SEA: THE ROLE OF TEMPERATURE AND ALGAL COMMUNITY STRUCTURE

Y. Afeworki, J.J. Videler, & J. H. Bruggemann

Abstract Coral reefs are characterized by intense herbivory. Spatial patterns in herbivory – particularly along the depth gradient – influence the distribution and abundance of algae. Depth gradients in herbivorous reef fishes are generally assumed to be temporally stable but this assumption has rarely been questioned. Here we use underwater visual census and herbivore exclusion experiments to study the community composition and temporal patterns in habitat use by roving herbivorous fishes in an environment characterized by profound seasonal changes in algal biomass and distribution and extreme summer temperatures. Among the 18 species of roving herbivores recorded, parrotfishes were dominant in species richness and biomass, while regional endemic species represented 77% of the total biomass. During most of the year, roving herbivores aggregate in the shallow reef zones and their biomass declines with depth. The herbivore community on the reef flat is distinct from that in deeper zones. The former is characterized by *Siganus rivulatus*, *Acanthurus gahhm* and *Hipposcarus harid*, while the deeper reef zones are characterized by *S. ferrugineus*, *Chlorurus sordidus* and *Ctenochaetus striatus*. In summer, the distinct community structures among reef zones are lost as reef flat herbivores tend to exploit deeper reef zones and some reef crest species venture on to the reef flat. This summer change in herbivore distribution is also reflected in reduced turf biomass and increased yield to herbivores in the deeper reef zones. Habitat use is related to the feeding mode such that browsers dominate the reef flat and scrapers the reef crest, while the seasonal changes correspond to changes in availability of targeted algal resources. These seasonal changes appear to be driven by the extreme temperatures in summer, reaching 36°C on the shallow reef flat.

Coral reefs (2013) 32:475–485

2.1 Introduction

Herbivory is an important force structuring benthic communities of coral reefs (Steneck 1988). Herbivores mediate the competition between corals and algae by causing favourable conditions for coral recruitment and growth (e.g., Mumby et al. 2007), prevent excessive growth of macroalgae (e.g., Hughes et al. 2007) and may facilitate reversal of benthic communities into a coral dominated state (e.g., Bellwood et al. 2006). Maintenance of high herbivore diversity is considered to augment the resilience of coral reefs to disturbance (Bellwood et al. 2004; Burkepile & Hay 2008). This is in part due to the diversity in feeding mechanisms of reef herbivores (Choat 1991) with varying impact on the benthos (Hixon & Brostoff 1996; Burkepile & Hay 2010). Moreover, some key ecosystem functions such as macroalgal consumption or bioerosion may be covered by only one or few species (Bellwood et al. 2003; Hoey & Bellwood 2009).

Difference in habitat use among reef herbivores may cause marked variation in grazing pressure among coral reef habitats. Species-specific preferences for certain reef zones appears to be common on coral reefs and the patterns are influenced by numerous factors including food choice, interference competition, predation and hydrodynamics (Robertson & Gaines 1986; Fox & Bellwood 2007). Whatever the drivers, the vertical zonation of herbivores is known to influence the distribution of benthic algae on coral reefs (Hay 1981b; Fox & Bellwood 2007).

Seasonal changes in vertical distribution and community structure of fishes are ubiquitous in temperate rocky shores and reefs (Ebeling & Hixon 1991; Zander et al. 1999). Temporal stability of habitat use patterns in tropical reef fishes is often assumed (Russ 1984b; Letourneur 1996), but has rarely been tested. Seasonal changes in habitat use and community structure of tropical reef fishes may be prevalent on coral reefs which experience significant seasonality. Indeed many coral reefs are influenced by monsoons or upwelling which cause variations in environmental conditions that drive dramatic changes in composition and abundance of benthic algae (Diaz-Pulido & Garzon-Ferreira 2002; Ateweberhan et al. 2006a). The effect of these seasonal variations on fish populations and in particular on the habitat use of herbivorous fishes has not been studied.

The highly seasonal environment of the southern Red Sea (Sheppard et al. 1992) is suitable to investigate the effects of changing conditions on coral reef ecological processes. In this region, shallow reef zones are characterised in the cool season (November – April) by high cover and biomass of canopy-forming and foliose macroalgae, whereas the hot season (May – October) algal turfs dominate (Ateweberhan et al. 2006a). Ateweberhan et al. (2006a) reported increases in turf algae biomass in summer on the shallow reef flats but concomitant decreases in the deeper reef zones. These authors hypothesized that grazing activity partly shifts from shallow to deeper zones during the hottest months. They attributed this to the movement of reef flat herbivores to the deeper reef zones, possibly driven by high temperatures and/or increased predation risk due to reduced habitat complexity in summer. In this study we use visual census and herbivore exclusion experiments to describe the community structure and patterns of habitat use by roving herbivorous fishes and to test whether these vary seasonally.

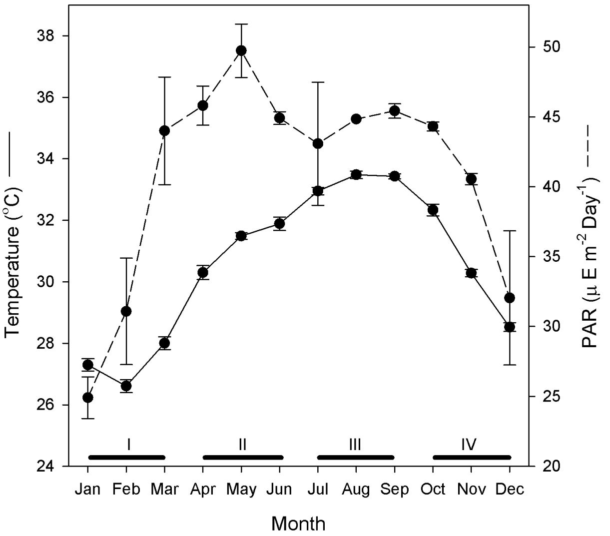

Fig. 2.1 Sheik Said Island southern Red Sea, Eritrea: mean monthly water temperature and surface irradiance. Fish counting periods are indicated in roman numerals.

2.2 Materials and methods

2.2.1 Study site and environmental setting

The study was conducted between July 2006 and May 2008 on the fringing reef of Sheikh Said Island near Massawa, Eritrea (15°35′N; 39°29′E) (see map in the Supplementary Material, Fig. S2.1.1). This 1 – 10 m deep reef has a gently sloping profile and a 30 – 45 m wide coral growth zone. Four reef zones were identified based on the topography and the composition of benthic communities: the reef flat (0 – 1 m), the reef crest (0 – 2 m), the shallow fore reef (2 – 6 m), and the deep fore reef (6 – 10 m). For detailed description of the substrate and biotic communities of the zones see Ateweberhan et al. (2006a) and Afeworki et al. (2011).

Field measurement of sea surface temperature and surface irradiance at the study site (see Supplementary Material S2.3 for details) indicate significant seasonal changes in both parameters (Fig. 2.1). The mean monthly water temperature (at 2 m depth) ranges from 27.7°C in January to 33.4°C in September (Ateweberhan et al. 2006a), with summer temperatures regularly exceeding 36°C on the reef flat (Ateweberhan et al. 2005a). Tides are semidiurnal with a mean amplitude of 0.7 m.

2.2.2 Turf biomass and yield to herbivores

Turf algae biomass and yield to herbivores were assessed on the reef crest; the shallow fore reef and the deep fore reef zones every 2 – 3 months from September 2007 to April 2008.

Horizontal surfaces of the dominant dead coral substrates were selected i.e.dead *Porites* colonies on the reef crest and shallow fore reef and dead *Echinopora* colonies on the deep fore reef (Afeworki et al. 2011). At least four such large dead coral substrates covered by turf algae (100% cover) were selected haphazardly for each month x zone combination. Small (10×10×3 cm) cages of galvanized mesh wire (mesh size 1 cm) were used to exclude a small part of each dead coral (<1/5th of the total surface) from grazing by roving herbivorous fishes, while substrates outside cages remained accessible to such herbivores. Sea urchins are rare on the study site and their grazing impact is assumed to be minimal. At the end of 3 – 6 days, pieces of substrate from inside and outside the cages were chiselled off, placed in separate plastic bags and kept chilled during transport to the lab. Turfs were carefully removed using a scalpel; taking care not to include substrate bound endolithic or crustose coralline algae. A piece of aluminium foil of known areal density was modelled over the substrate and carefully trimmed to match the irregular edges of the substrate sample. The surface area was then estimated by dividing the mass of the piece by the mass per unit area of the aluminium foil. To determine the ash free dry mass (AFDM), samples were dried at 60°C, and ashed at 550°C in a muffle furnace for 8.5 hrs.

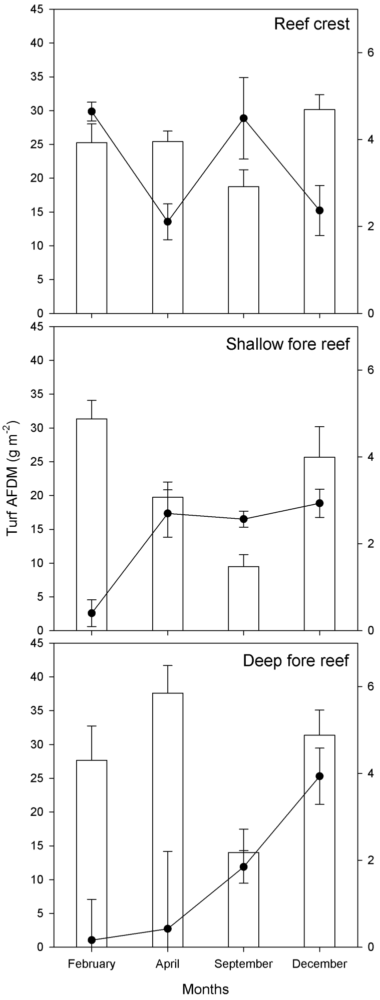

Fig. 2.2 Spatial and temporal patterns in turf algae biomass and yield to herbivores at Sheikh Said Island, southern Red Sea, Eritrea. Bars are mean ±SE of turf biomass. Dots are mean ±SE of yield to roving herbivores.

Based on feeding preferences, roving herbivores are classified into scrapers/small excavators, macroalgal browsers and grazers (Green & Bellwood 2009). Specifically, *Kyphosis vaigiensis*, *Siganus luridus*, and *S. rivulatus* are identified as macroalgal browsers, *Acanthurus gahhm*, *A. sohal*, *Ctenochaetus striatus*, and *Siganus stellatus* as grazers, *Hipposcarus harid*, *S. collana*, *S. ferrugineus* and *Chlorurus sordidus* as scrapers.

Previous studies have demonstrated that the effects of caging on the biomass and species composition of turf algae, on irradiance and on water flow are negligible (e.g., Hixon & Brostoff 1985; Smith et al. 2001; Vermeij et al. 2010). Therefore, and given to the short duration of the experiments, cage controls were not used in the present study.

2.2.3 Density and biomass of roving herbivorous fishes

Species-level visual censuses of the roving herbivores from the families Acanthuridae (surgeonfishes), Kyphosidae (rudderfishes), Labridae (parrotfishes), and Siganidae (rabbitfishes) were conducted along belt transects by snorkelling on the reef flat and reef crest and by using SCUBA in the shallow fore reef and deep fore reef zones. In each zone six replicate 30×5 m transects were haphazardly laid out and their positions permanently marked using metal stakes hammered into the substrate. Individual fishes were identified and placed in 5 cm size categories. Estimation of fish size was practiced outside the study area using PVC pipes of various lengths and by spearing fish whose size was estimated underwater beforehand. Mean error and precision in length estimation were 0.51 cm and 2.5 cm respectively. Seasonal effects were investigated by conducting censuses during each of four periods: January to March (I), April to June (II), July to September (III), and October to December (IV) (Fig. 2.1). All censuses were conducted by the same observer (Y.A.) between 1000 hrs and 1600 hrs at high tide, to minimize variation associated with tidal movements of fishes (Table S2.7.1, Figs. S2.7.1 and S2.7.2). Fish densities were converted into biomass using length-weight relationships (Table S2.4.1) taking the midpoint of each size class.

2.2.4 Data analysis

Variation in biomass and yield of turf algae biomass were examined among zones and seasons using ANOVA and untransformed data. Variation in total density/biomass of all roving herbivores and that of the individual species were tested by a Repeated Measures ANOVA (RMA) taking zone as a between subject factor and period as repeated measure. For all the parametric tests, normality of data were tested with the Kolmogorov-Smirnov goodness of fit test and equality of variances using the Levene's test. Fish density data were log transformed and biomass data were square root transformed to fulfil the assumptions of parametric tests. Assumption of sphericity was tested by Maculay's sphericity test and the Greenhouse-Geisser correction was applied when that assumption was violated. Multiple comparisons between zones were tested using Tukey's honestly significant test.

Differences in community structure of roving herbivores among zones were tested using permutation based analyses of similarity (ANOSIM) on Bray-Curtis similarities between square root transformed biomass values. Among-zone variation in the composition of species and functional groups was further investigated by principal components analysis (PCA) of the square-root transformed biomass data. The effect of the repeated measure, period, and its interaction with zone was assessed using second stage community analysis (Clarke et al. 2006).

2.3 Results

2.3.1 Turf biomass and yield

Biomass of turf algae and yield to herbivores varied among reef zones and with time of year, and showed significant zone*month interaction (Fig. 2.2, Table S2.5.1). On the reef crest, turf biomass remained the same except for a slight decrease in September. On the shallow fore reef, biomass of turfs declined gradually from the cool to the hot season, with the lowest biomass in September. On the deep fore reef, turf biomass remained high throughout the year except during September when there was a sharp drop.

Overall, yield was highest on the reef crest and lowest on the deep fore reef, but this varied among periods. While yield on the reef crest remained high in all months, it increased from lowest values in February to higher yields during the warmer parts of the year in the two deeper zones. Overall, yields were highest in September and December.

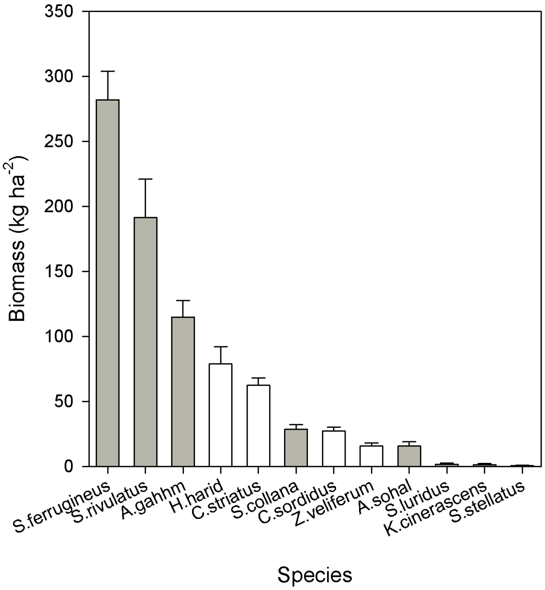

Fig. 2.3 Regional endemics dominating roving herbivore biomass at the fringing reef of Sheikh Said Island Eritrea. Bars represent mean biomass (±SE) averaged over four reef zones and four periods. Grey bars: regionally endemic species; open bars: widespread species.

2.3.2 Spatial and temporal variation of total abundance of roving herbivores

A total of 18 species of roving herbivores were encountered in the course of the study, comprising 9 parrotfishes, 3 rabbitfishes, 5 surgeonfishes, and one rudderfish (Table S2.6.1). Six of these were rare and are not considered further (Table S2.6.1). Among the 12 common species, five are endemic to the Red Sea and the Arabian Sea: *A. gahhm*, *A. sohal*, *S. ferrugineus*, *S. collana*, and *S. rivulatus*. Together, these regional endemics represent 77% of total roving herbivore biomass (Fig. 2.3; see Box 2.1 for a discussion of endemism and population size). Averaged over all zones, the two dominant roving herbivores on this fringing reef are *S. ferrugineus* and *S. rivulatus*, representing respectively 34% and 23% of the total biomass (Fig. 2.3, Table S2.6.1). Among the four families investigated, parrotfishes were the dominant group both in terms of species richness and biomass representing 51% of the total reef wide roving herbivore biomass (Table S2.6.1).

Box 2.1 Endemic marine species are locally the most abundant

The geographical range of species and their abundance is positively correlated in terrestrial ecosystems (Blackburn et al. 1997; Gaston et al. 1997). Stated differently, endemic species are typically the least abundant in their locality. In the southern Red Sea, the endemic herbivorous fishes were the dominant taxa in their habitat (Fig. 2.3). Similar observations were recorded in butterflyfishes and angelfishes in which the endemic species such as *Chaetodon larvatus* are the most dominant taxa (Zekeria & Videler 2000; Zekeria et al. 2005). Dominance of endemic species at this site agrees with the general observations elsewhere in the marine environment (Hourigan & Reese 1987; Hobbs et al. 2010; Hobbs et al. 2011). Because of this, abundance and range-size are negatively correlated in the marine environment (Jones et al. 2002). The above difference between terrestrial and marine ecosystems, suggests that factors that determine extinction and speciation patterns in the marine and terrestrial ecosystems may differ.

In general extinction rate is higher in rare species (small range size and low local density) and when stochasticity is high (Gaston 1998; Johnson 1998). Hobbs et al. (2010) suggest that large local population in endemics is an insurance against extinction risk due to the highly stochastic nature of marine fish populations. The stochasticity of marine populations is a direct outcome of their bi-partite life style, i.e. the pelagic larval phase and an adult sedentary phase. The pelagic phase experiences high mortality rates as a result of which spatial and temporal patterns in recruitment in marine organisms are highly variable (Doherty & Williams 1988; Doherty 2002). It appears that endemic marine organisms minimize this risk by maintaining large local populations. Some relevant adaptations that have been observed in this regard are: shorter larval duration, higher reproductive output and local retention of recruitment in endemic species (Eble et al. 2009; Crean et al. 2010; van der Meer et al. 2012).

Roving herbivores had a non-uniform distribution across the four reef zones and their distribution among zones varied with period (significant period*zone interaction) (Fig. 2.4, Table S2.6.2). Total herbivore density ranged from a maximum of 15267±3416 ind. ha^{-1} on the reef flat to a minimum of 433±261 ind. ha^{-1} on the deep fore reef (Table S2.6.1). The corresponding values for biomass were 1479±728 kg ha^{-1} on the reef flat and 77±62 kg ha^{-1} on the deep fore reef (Table S2.6.1). Overall, total density and biomass were highest in the two shallowest zones, intermediate on the shallow fore reef and lowest on the deep fore reef. Although the density of roving herbivores was lower on the reef crest than on the reef flat, the biomass was similar in both zones due to the fact that the reef crest supported larger bodied fishes than the reef flat.

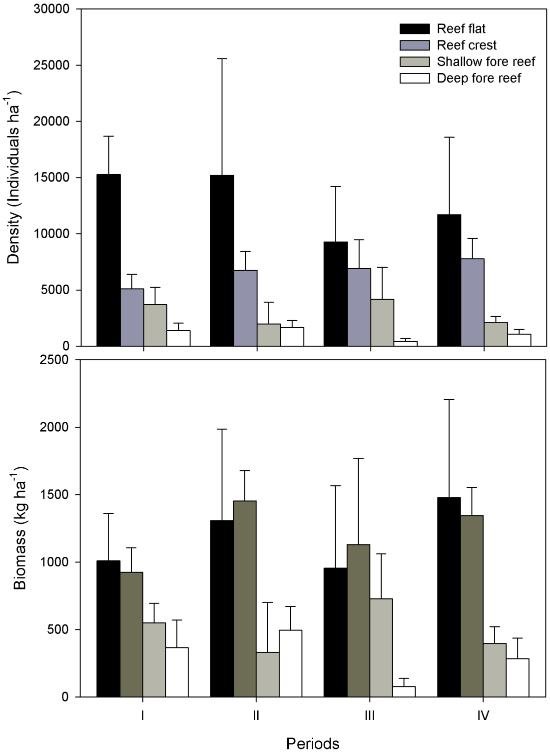

Fig. 2.4 Total roving herbivore density and biomass in four reef zones during four periods at Sheikh Said Island, southern Red Sea, Eritrea. I: January – March; II: April – June; III: July – September; IV: October – December. Bars indicate means and their 95% confidence interval.

For each period, a post-hoc test for zone was conducted to interpret the period*zone interaction term. Distribution of roving herbivores among zones remained the same throughout the year except during the hot July to September period when the shallow fore reef supported similar herbivore density and biomass as the two shallowest zones (Fig. 2.4). In all periods the deep fore reef supported the lowest number of herbivores except during the cool January to March period when total density equals that on the shallow fore reef. In summary, roving herbivores aggregate in the two shallowest zones (reef flat and reef crest) except during the hottest months when the shallow fore reef supports similar abundance as the two shallower zones.

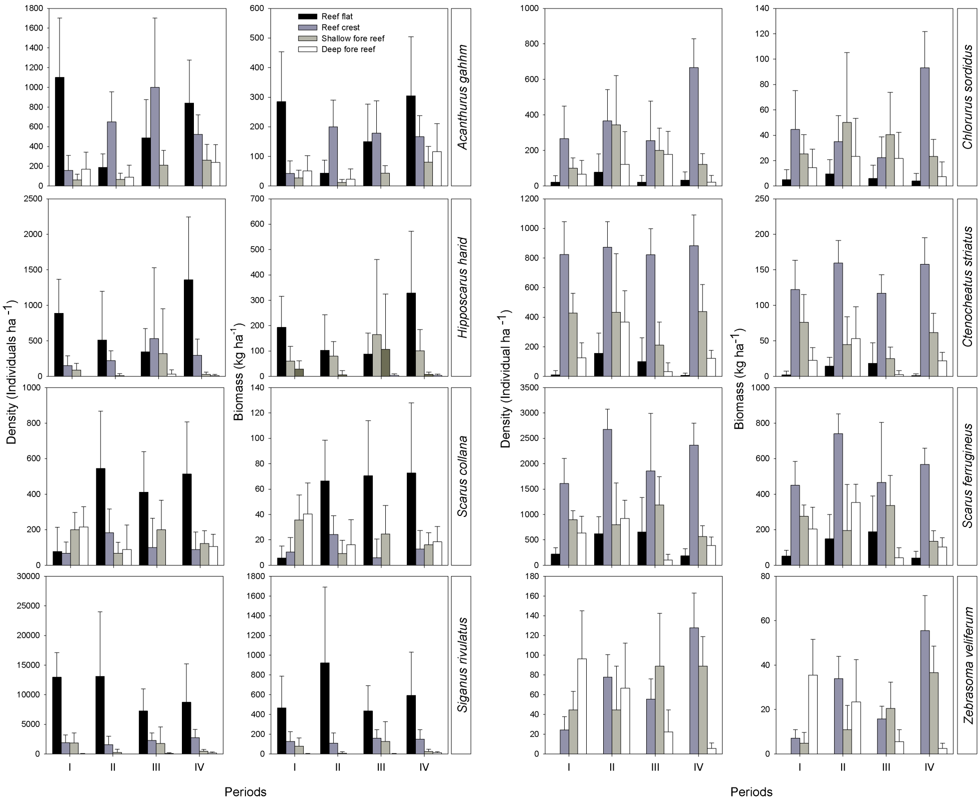

Fig. 2.5 Roving herbivorous fishes of Sheikh Said Island, southern Red Sea, Eritrea. Seasonal patterns in the distribution of biomass and abundance among four reef zones. Left hand panels show roving herbivores that are dominant on the reef flat; right hand panels represent those that have highest abundance on the reef crest. I: January – March; II: April – June; III: July – September; IV: October – December. Bars represent mean values and 95% confidence interval.

2.3.3 Roving herbivorous fish communities and their seasonal changes

Numerically browsers were the dominant group, accounting for 56% of the total count, followed by scrapers (30%) and grazers (14%). In terms of biomass, scrapers were dominant, representing 51% of total biomass, twice as much as browsers (24%) and grazers (25%).

RMA tests of all the investigated species showed that their abundance varied significantly among zones (Figs. 2.5) (Table S2.6.3). This was reflected in the community composition of roving herbivores which differed significantly among zones (ANOSIM: Global R = 0.615, P = 0.001). Also PCA showed clear among-zone differences in the composition of species and functional groups (Fig. 2.6). The first two axes explained 85.2% and 93.5% of the variation for the analysis based on species and functional groups respectively. Along the first principal

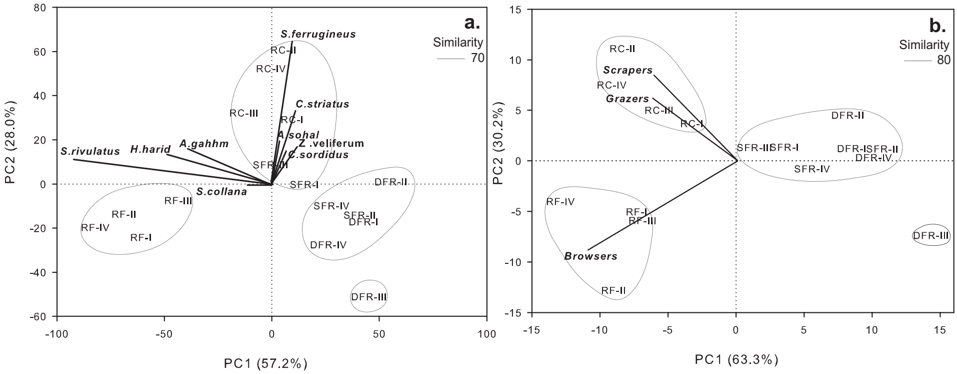

Fig. 2.6 Roving herbivorous fishes of Sheikh Said Island, southern Red Sea, Eritrea. Principal components analysis showing the variation in the composition among four reef zones at the level of species (a) and of feeding functional groups (b). Vectors show the correlation of species and/or functional group with the principal axes. RF: reef flat, RC: reef crest, SFR: shallow fore reef, DFR: deep fore reef. I: January – March; II: April – June; III: July – September; IV: October – December.

axis, the reef flat was distinct from the other reef zones being characterized by *S. rivulatus*, *H. harid*, *A. gahhm* and *S. collana* (Fig. 2.6a). Along the second principal axis the high biomass of scrapers (mainly *S. ferrugineus*) and to a lesser extent that of grazers (mainly *C. striatus*) differentiated the reef crest from the reef flat and deeper zones (Fig. 2.6a). The reef flat was positively associated with browsing due to the high biomass of *S. rivulatus* (Fig. 2.6b) and the reef crest with scrapers and grazers.

Seasonal change in habitat use is reflected in the MDS plots which indicate that the herbivore community of the reef flat remains distinct for much of the year except during the hottest months from July to September when the community structure of the reef flat becomes similar to that of the reef crest and shallow fore reef (Fig. 2.7). Cluster analysis based on the second stage similarity matrix (derived from the similarity matrices of the four periods) confirms the above results: species distribution among the four reef zones during July to September is most dissimilar from species distributions during the other times of year (Fig. 2.7). Six species were responsible for this seasonal change in habitat use as indicated by the significant zone*period interaction in the RMA (Fig. 2.6, Table S2.6.3). These were *A. gahhm*, *C. striatus*, *C. sordidus*, *S. collana*, and *S. ferrugineus*.

2.4 Discussion

2.4.1 Regional comparisons of herbivore community structures

The roving herbivore community of the fringing reef of Sheikh Said Island is strikingly different from those in the northern Red Sea. There, browsing rabbitfishes represent <2% of

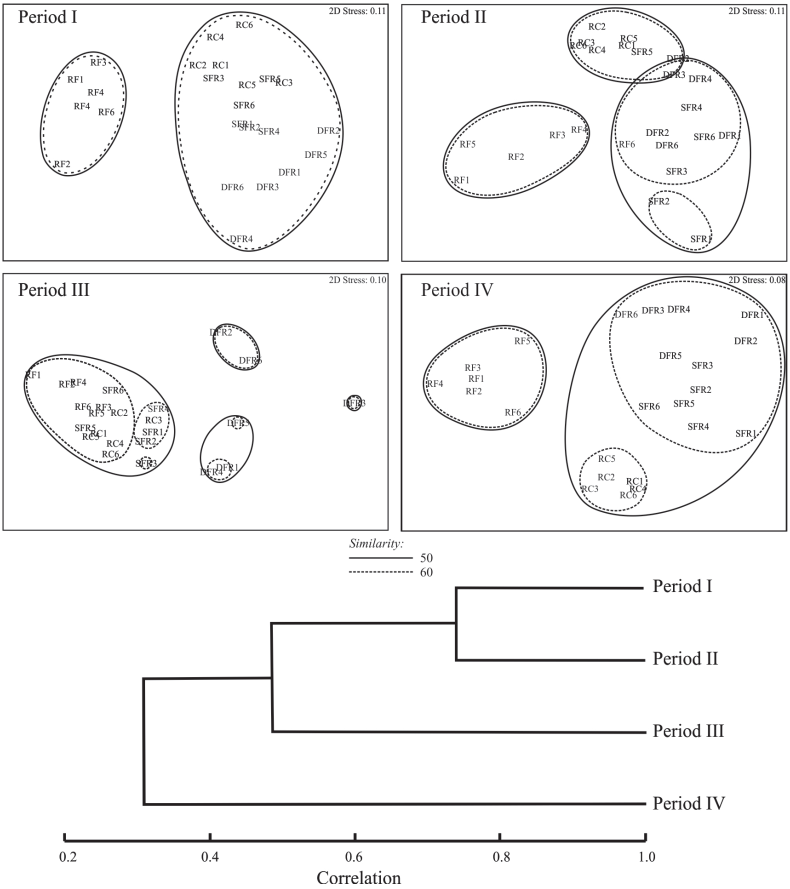

Fig. 2.7 Seasonal changes of the structure of the roving herbivore community among four reef zones at Sheikh Said Island, southern Red Sea, Eritrea. MDS plots based on first stage similarity matrices are shown for each season. The cluster analysis is based on second stage similarity matrix. RF: reef flat, RC: reef crest, SFR: shallow fore reef, DFR: deep fore reef. Numbers indicate replicate transects at each zone. I: January – March; II: April – June; III: July – September; IV: October – December. Figure by John Videler.

all roving herbivores, excavating parrotfishes are well represented both in terms of diversity and abundance, and reef flats are dominated by grazing/detritivorous surgeonfishes such as *Acanthurus nigrofuscus* and *A. sohal* (Bouchon-Navaro & Harmelin-Vivien 1981; Alwany et al. 2009; Brokovich et al. 2010). In contrast, our study site in the southern Red Sea supports large populations of the browsing *S. rivulatus*, scraping parrotfishes *S. ferrugineus*, *S. collana* and *H. harid* dominate herbivore biomass and there is a high abundance of the grazing surgeonfishes *A. gahhm* and *C. striatus*. Large excavating parrotfishes are absent. This may be typical of the southern Red Sea, as similar patterns of community composition were observed on the fringing reefs in the Gulf of Zula, located 80 km to the south of the present study site (Y.A. pers obs).

S. rivulatus feeds primarily on erect macroalgae (Lundberg & Lipkin 1979) and is known to cause seasonal reduction in macroalgal biomass (Ateweberhan et al. 2006a; Sala et al. 2011). The high abundance of this species appears to be associated with the availability of extensive macroalgal beds in the southern Red Sea (Sheppard et al. 1992; Turak et al. 2007). These macroalgal beds experience massive seasonal shedding that enriches the detrital pool (Ateweberhan et al. 2005a; Ateweberhan et al. 2006b; Ateweberhan et al. 2006a). Since a substantial proportion of the food that scrapers and grazers ingest is detritus (Choat et al. 2002; Choat et al. 2004), the large biomasses of these functional groups recorded here may be associated with the increased availability of detritus. These findings suggest different trophic structures on coral reefs in the southern and northern Red Sea, particularly regarding the importance of browsing and detritivory.

The gradients in environmental conditions and herbivore communities along the south-north axis of the Red Sea are comparable to the inshore-offshore gradients of the GBR. The inshore reefs of the GBR, due to high turbidity, high nutrient levels and large macroalgal stands are comparable to the southern Red Sea reefs while the northern Red Sea reefs, having deeper waters, more developed and diverse coral taxa and low cover of macroalgae resemble those of the outer shelf reefs of the GBR (Roberts et al. 1992; Sheppard et al. 1992; Wismer et al. 2009; De'ath & Fabricius 2010). Reefs with abundant macroalgae support larger populations of browsers, grazers and scrapers (Williams & Hatcher 1983; Russ 1984a; Cheal et al. 2012) while excavating taxa are more diverse and abundant on the coral rich sites (Hoey & Bellwood 2008; Alwany et al. 2009). These resemblances suggest that herbivore communities may vary in a predictable manner depending on the environmental conditions and associated state of the benthic communities. For example it is plausible that the relative abundance of excavators and scrapers may be influenced by the diversity and cover of scleractinian corals since excavators feed more on live corals than scraping taxa (Bellwood & Choat 1990; Francini et al. 2008; Alwany et al. 2009). Likewise browsers and detritivores will be expected to be abundant in the macroalgae dominated areas (Ferreira et al. 2004; Hoey et al. 2011) where high amounts of detrital matter are generated. The importance of variation in these food sources and their nutritional quality for shaping the community structure of roving herbivores has not been investigated (Clements et al. 2009). Clearly, more detailed studies are needed to understand the role of diet and availability of resources in shaping these communities.

2.4.2 Depth related changes in herbivore abundance and composition

The decline in herbivore biomass and grazing intensity with depth is common to all coral reefs and appears to be associated with lower temperature, reduced algal productivity and increased predation risk in deeper waters (Hay et al. 1983; Russ 2003; Fox & Bellwood 2007; Brokovich et al. 2010). Lack of shelter and presence of large predators in deeper waters could deter herbivores from foraging at deeper reef zones (Parrish & Boland 2004; Leichter et al. 2008). However, at our study site topographic complexity of the deep fore reef zone is similar to that of the shallower zones and higher than that on the reef flat (Fig. S2.1.1), yet this zone supports the lowest biomass of roving herbivores. It is therefore unlikely that lack of shelter causes the depth-gradient in herbivore abundance.

In contrast, both temperature and primary production are correlated with depth and both are known to influence grazing intensity (Cebrian & Lartigue 2004; Smith 2008). For the depth range covered in this study (0 – 10 m), a steep decline in algal productivity owing to the diminishing light levels can be expected (see Vine 1974; Hay 1981b; Klumpp & Mckinnon 1992), while the associated drop in temperature will be small with a negligible effect on consumption rates (e.g., Brokovich et al. 2010). Hence, reduced algal productivity is likely the main driver of declining herbivore biomass with depth. The observation that the taxa that incorporate the most living plant matter in their diet show the greatest decline in abundance with depth (Choat et al. 2004) underpins the role of primary productivity.

Species interaction is unlikely to have contributed to community differences as all investigated taxa are none-territorial roving herbivores forming multispecies groups (with the exception of relatively uncommon *A. sohal*). It is also unlikely that differences in hydrodynamics between the reef flat and the reef crest drive community differences as the study site is located in a sheltered bay and the area in general is known for its calm conditions.

The reef flat and reef crest zones do differ in the composition of benthic algae and in topographic complexity. The reef flat has the lowest topographic complexity and is dominated by erect foliose and canopy-forming macroalgae during the cool season (Ateweberhan et al. 2006a). The reef crest is largely dominated by crustose corallines, turf algae and living corals (Ateweberhan et al. 2006a; Afeworki et al. 2011). A combination of feeding preferences and anti-predator adaptations appears to determine how these species use the reef zones.

2.4.3 Seasonal changes in habitat use patterns

We report significant seasonal changes in community structure of roving herbivorous fishes among depth zones. Our results differ from other findings where spatial patterns persist over time, implying stability in habitat use among reef fishes (Russ 1984b; Letourneur 1996; Brokovich et al. 2006). The discrepancy may be due to the highly seasonal nature of the southern Red Sea. Shallow reef flats in this region experience extreme summer temperatures that effect dramatic changes in benthic community, alternating between a canopied state in the cool season to a turf-dominated flat expanse in summer (Ateweberhan et al. 2006a). In summer, scrapers and grazers can potentially benefit from the increased availability of this resource on the reef flat. Indeed, typical reef crest herbivores, i.e., the detrivorous *C. striatus*, and the scrapers *C. sordidus* and *S. ferrugineus* slightly increased their abundance on the reef flat in summer. Interestingly, the scraper *S. collana* mainly forages on the reef flat for most of the year except during the cool season when its peak abundance shifted to deeper reef zones. This species apparently avoids the reef flat during the period of peak canopy development by macroalgae, possibly due to lack of food resources or due to the deterrent effect of dense macroalgal stands (Hoey & Bellwood 2011). Thus, the patterns of seasonal change in habitat use by these species appear to be correlated to their feeding modes.

It is notable that the reef crest species such as *S. ferrugineus* and *C. striatus* fail to respond to the seasonal increase in turf biomass on the reef flat. Previous studies have suggested that such patterns may be related to the lack of shelter and increased risk of predation on the reef flat (e.g., Randall 1965; Nemeth & Appeldoorn 2009; Verges et al. 2011). Interestingly, the roving herbivores that dominated the reef flat are schooling species with drab colouration, two characteristics that have been hypothesized to reduce predation risk (Montgomery et al. 1989; Borsa et al. 2007). Abundant resources on the one hand and predation risk on the other may represent a strong selective pressure for cryptic coloration and the tendency for schooling in species that frequent the topographically less complex portions of the reef. Indeed this is considered the major cause in the radiation of two distinct life styles in the family Siganidae: the drab, fusiform reef flat frequenting species such as *S. rivulatus* and the more reef associated deep bodied and colourful ones such as *S. stellatus* (Borsa et al. 2007).

During summer water temperatures on the reef flat of our study site regularly exceed 36° C (Ateweberhan et al. 2005a), values which are considered to be critical for resident coral reef fishes in other locations (Mora & Ospina 2001; Eme & Bennett 2009). It is possible that the observed seasonal change in habitat use patterns in roving herbivores may be related to these extreme temperatures and to species- or size-related differences in temperature tolerance. In summer we recorded lowered turf biomass and increased yield to grazers in deeper zones. Previously, records have shown an opposite trend on the reef flat with higher accumulation of biomass of turfs and increased survivorship of primary laterals of macroalgae (Ateweberhan et al. 2005a; Ateweberhan et al. 2006a). These observations suggest a transfer in grazing pressure from shallow to deeper reef zones in summer that may partly be due to the extreme temperatures at the shallow reef zone. However, our census data only showed a negligible seasonal shift of roving herbivore biomass to the shallow fore reef in summer. The discrepancy between grazer impact and census suggests that a more frequent (monthly) and direct assessment of herbivore impact (such as by video) is needed. Moreover assessment of temperature tolerance by roving herbivores is required to clarify the role of temperature. In any case, reduced herbivore impact on the reef flat during summer has the potential to provide reef flat macroalgae a refuge from grazing during part of the year, leading to recruitment success and/or lowered grazing-induced loss of primary laterals.

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A2 Appendix

A2.1 Global patterns in biomass of coral reef grazers

Grazer biomass at the study site was compared to values obtained for other coral reefs from different geographic regions and management regimes (see below for a list of the studies considered). For each region, grazer biomass data were considered only if obtained from underwater visual census and if management status of the reef was clearly indicated. Management regimes were classified as: open, fished areas, marine reserves and remote locations with minimal human impact. Biomass estimates were standardized by converting values into kg ha^{-1}. Long term data on grazer abundance from fished and protected reef areas is available for the Western Indian Ocean (McClanahan & Graham 2005; McClanahan et al. 2007), the Central Indo-Pacific (Stockwell et al. 2009) and the Caribbean (Williams & Polunin 2001; Newman et al. 2006). For the Central Pacific Islands remote uninhabited islands were taken as none impacted reefs while those close to human habitation were considered as impacted (following Friedlander & DeMartini 2002; Albert et al. 2008; DeMartini et al. 2008). The inner shelf reefs of the Great Barrier Reef are regarded as impacted by anthropogenic factors, while the mid shelf and outer shelf reefs are considered less impacted reefs (Pandolfi et al. 2003).

List of published studies with estimates of biomass of grazing reef fishes from different regions that were considered for the comparison are:

1. **Caribbean**: Bruggemann (1994); Williams and Polunin (2001); Hawkins and Roberts (2004b); Newman et al. (2006)
2. **Central Indo-Pacific**: Stockwell et al. (2009)
3. **Great Barrier Reef**: Russ (2003); Fox and Bellwood (2007); Fox and Bellwood (2008a); Wismer et al. (2009); Hoey and Bellwood (2010)
4. **Pacific Islands**: Labrosse et al. (1999); Friedlander and DeMartini (2002); Wantiez and Chauvet (2003); DeMartini et al. (2008); Albert et al. (2008)
5. **Northern Red Sea**: Brokovich et al. (2010)
6. **Western Indian Ocean**: Jennings et al. (1995); McClanahan (1997); McClanahan and Graham (2005); Ledlie et al. (2007); Nordemar et al. (2007); McClanahan et al. (2007); McClanahan et al. (2009b)

Grazer biomass ranged from minimum values at extensively fished sites to maximum values on the outer-shelf sites of the Great Barrier Reef (GBR) (Fig. A2.1.1). With the exception of the Pacific Islands, fished sites harboured significantly lower grazer biomass than unfished sites (Fig. A2.1.1). Remote un-impacted Pacific Islands have low grazer biomass because of high rates of predation (inverted throphic pyramid) due to the large number of top predators present (DeMartini et al. 2008).

The southern Red Sea harbors one of the highest biomass of grazers recorded in coral reefs and is comparable to the outer shelf reefs of the Great Barrier Reef (Fig. A2.1.1). In addition grazer impact expressed as yield to grazers at our study is 0.8 – 1.4 g Carbon m^{-2} d^{-1}

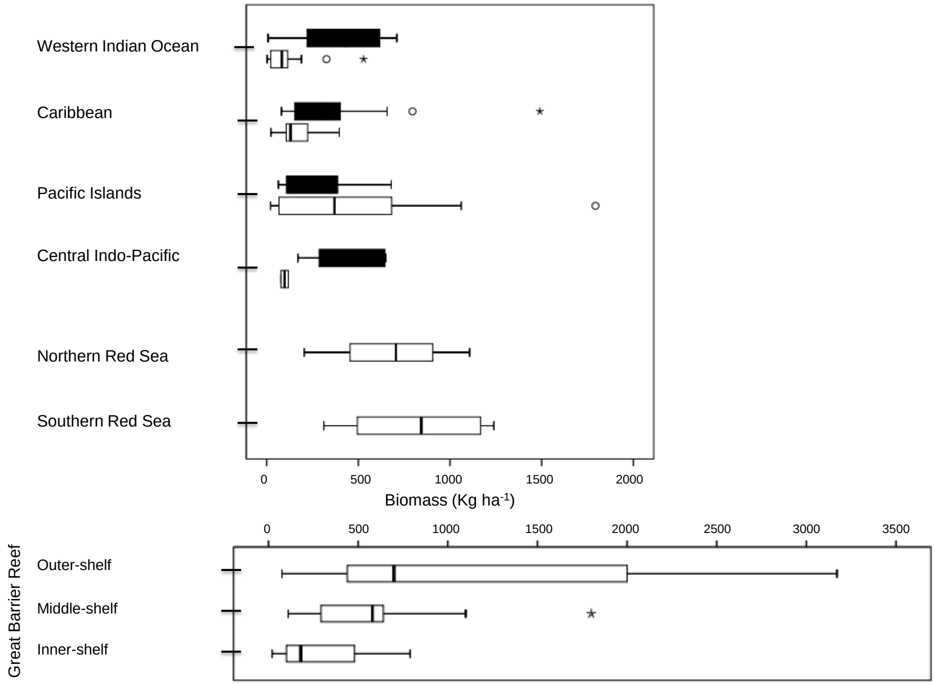

Fig. A2.1.1 Global pattern in grazer biomass. Open bars: no-take areas where fishing is prohibited, dark bars: fished sites. Grazer biomass of the Great Barrier Reef is shown separately due to extreme values of the outer shelf reefs.

(taking a 40.5% conversion factor from AFDM to Carbon (Bruggemann et al. 1994)). These figures are within the range of values reported for the densely populated outer shelf reefs of the GBR (Russ & McCook 1999; Russ 2003). The large grazer biomass in the southern Red Sea is attributable to low fishing intensity and high benthic primary productivity. Fishing in the coastal areas of Eritrea is largely artisanal with exploitation levels estimated to be less than 10% of the maximum sustainable yield (Tsehaye et al. 2007). Moreover fishing on scarids, acanthurids, and siganids is virtually absent as these are traditionally not targeted. In terms of weight, over 96% of the catch is dominated by predatory species such as groupers, snappers, jacks and emperors (Tsehaye et al. 2007).

A further sign of the low fishing impact is the dominance of large sizes in all the studied species (see Supplementary material section S2.6 and Fig. S2.6.1). However, low fishing pressure alone cannot explain the high grazer biomass at the study site, because reefs in the southern Red Sea support twice as much grazer biomass as the no-take areas in Kenya that have been effectively protected for over 30 years (McClanahan et al. 2007). We believe that this is due to the higher primary production in the southern Red Sea (Veldhuis et al. 1997;

Ateweberhan et al. 2006a) compared to other coral reef locations. Two factors, namely, seasonal input of nutrient rich Indian Ocean water through the Bab el Mandeb and the broad shallow continental shelf of the southern Red Sea are primarily responsible for the high primary production in the southern Red Sea (Morcos 1970; Sheppard et al. 1992). Positive correlation between production (availability) of turf algae and grazer biomass has previously been shown (Carpenter 1990; Klumpp & Polunin 1990; Robertson 1991a). It is possible that over large spatial scales the upper limits of total grazer biomass may be set by productivity.

S2 Supplementary Material

S2.1 Study site

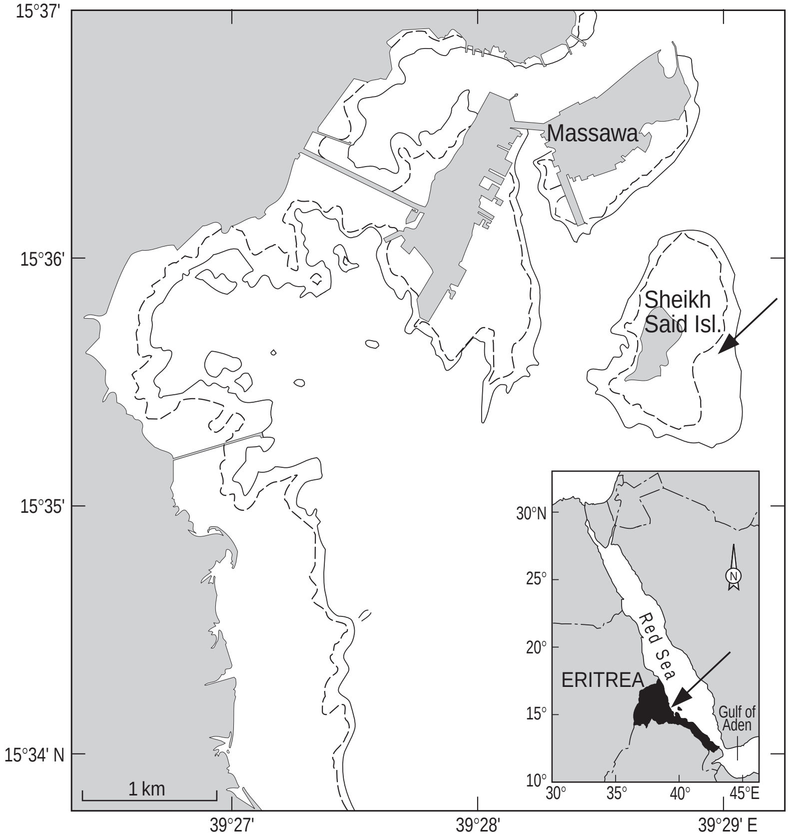

Fig. S2.1.1 Map of Massawa Eritrea showing the location of the study site. Figure by Dick Visser.

S2.2 Topographic complexity

The topographic complexity of the study site was estimated using a 3 m chain that was laid parallel and perpendicular to the reef crest at haphazardly selected sites, following the contours of the substrate. Sample size was 20, 42, 68, and 50 for the inner reef flat, the reef crest, the shallow fore reef and the deep fore reef zones respectively. Topographic complexity was calculated as the ratio of the length of the chain and the planar length measured. The topographic complexity was significantly different among zones (ANOVA: $F_{3,176} = 3.29$, $P = 0.022$), with the reef flat having the least and the reef crest having the highest complexity (Fig. S2.2.1).

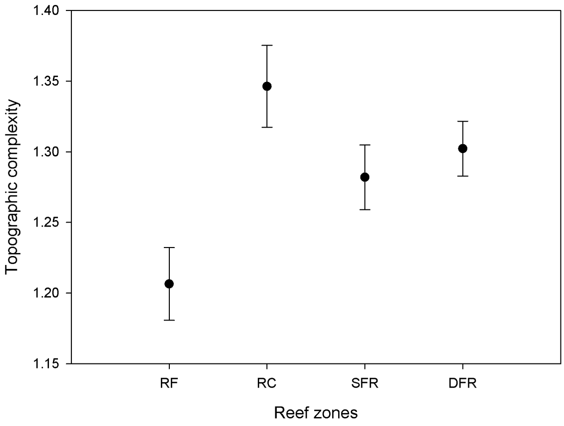

Fig. S2.2.1 Sheikh Said Island, southern Red Sea, Eritrea. Topographic complexity of the four reef zones investigated. RF: Reef flat; RC: Reef crest; SFR: Shallow fore reef; DFR: Deep fore reef.

S2.3 Environmental conditions

Hourly weather data, comprising as air temperature, wind speed and direction, gust speed and photosynthetically available radiation (PAR), were recorded between 2006 and 2008 using a weather station (HOBO onset technologies). The logger was located on the mainland at a location 1 km from the Sheikh Said Island and was mounted on a metal stake 4 m above ground. Instant PAR records were converted into daily integrated values and the mean monthly PAR in μE m^2 Day^{-1} were calculated. Sea surface temperature at the study site was recorded at two-hourly intervals at 2 m depth on the shallow fore reef zone between 2003 and 2006 (HOBO onset technologies).

S2.4 Length-weight relationships used in the study

Length-weight relationships for *Chlorurus sordidus*, *Ctenochaetus striatus*, *Hipposcarus harid*, *Scarus collana* and *S. ferrugineus* were derived from fish collected on the fringing reefs of Massawa near the study site (Table S2.4.1). Fish were collected either by barrier nets of by spearing. Their fork length and wet body mass were measured in the lab. Parameters of the length-weight relationship ($W = aFL^b$) were estimated by least squares regression in SPSS for Windows 16.0 (2007). For *Acanthurus sohal*, *A. gahhm*, *Kyphosus cinerascens*, and *Siganus stellatus* we used published parameters (Table S2.4.1) from the similar sized and closely related species *A. lineatus*, *A. nigricauda*, *K. vaigiensis* and *S. rivulatus* respectively.

Table S2.4.1 Length-weight relationships ($W = aFL^b$) used in the study; W = wet body mass (g), FL = fork length (cm) and a and b are parameters of the relationship.

Species	a	b	R^2	Location	Source
Acanthurus nigricauda	0.0261	3.024	0.99	New Caledonia	Letourneur et al. (1998)
Acanthurus lineatus	0.0251	3.03	0.99	American Samoa	Craig et al. (1997)
Ctenochaetus striatus	0.074	2.517	0.99	Eritrea, Red Sea	Present study
Zebrasoma veliferum	0.0339	2.855	0.98	New Caledonia	Letourneur et al. (1998)
Chlorurus sordidus	0.025	2.92	0.96	Eritrea, Red Sea	Present study
Hipposcarus harid	0.015	3.029	0.99	Eritrea, Red Sea	Present study
Scarus collana	0.105	2.411	0.99	Eritrea, Red Sea	Present study
Scarus ferrugineus	0.04	2.77	0.97	Eritrea, Red Sea	Present study
Siganus rivulatus	0.022	2.82	0.87	Egypt, Red Sea	Abdallah (2002)
Siganus luridus	0.011	3.04	0.82	Egypt, Red Sea	Abdallah (2002)
Kyphosus vaigiensis	0.02	3.037	0.99	New Caledonia	Kulbicki et al. (2005)

S2.5 Turf biomass and yield

Table S2.5.1 Summary of ANOVA results on biomass and yield to herbivores of turf algae at three reef zones (reef flat, shallow fore reef and deep fore reef) of the fringing reef of Sheikh Said, southern Red Sea, Eritrea. Turfs on dead coral substrates were sampled in February, April, September, and December. AFDM: ash free dry mass; df: degrees of freedom; MS: mean squares; *F*: ANOVA F- statistic; *P*: probability. Significant *P* values in bold type.

Effect	Turf biomass (AFDM g $\mathrm{m^{-2}}$)				Yield to grazers (AFDM g $\mathrm{m^{-2}d^{-1}}$)			
	df	MS	*F*	*P*	df	MS	*F*	*P*
Month	3	719.31	14.799	**0.000**	3	9.026	2.86	**0.045**
Zone	2	194.93	4.01	**0.023**	2	17.749	5.62	**0.006**
Month*zone	6	139.04	2.86	**0.016**	6	12.446	3.94	**0.002**
Error	59	48.61			55	3.156		

S2.6 Density, biomass, and size structure of roving herbivores

The study site has a diverse roving herbivore community (Table S2.6.1) dominated by *Scarus ferrugineus* and *Siganus rivulatus*. Density and biomass of *A. gahhm*, *C. striatus*, and *S. ferrugineus* varied significantly with period (Table S2.6.2). In *S. rivulatus* the change concerned density only, not biomass (Table S2.6.2). The other common species did not show intra-annual variation in density and/or biomass. Pairwise comparisons were conducted to identify the periods of peak density. *A. gahhm* had the highest density and biomass during October – December (Pairwise comparison: $P < 0.002$). Density of *C. striatus* was highest in April – June and its biomass was lowest in July – September (Pairwise comparisons: $P < 0.015$). Peak density and biomass of *S. ferrugineus* occurred in April – June and was significantly lower during the other periods (Pairwise comparisons: $P < 0.040$). Highest density in *S. rivulatus* was recorded during cool January – March (Pairwise comparisons: $P < 0.043$). In summary, the most abundant species at the study site all showed significant intra-annual variation in density and/or biomass.

Analysis of the size structure of these species suggests that recruitment pulses may have contributed to the difference among periods. The size structure of *S. rivulatus* in January – March was significantly different from that during the other periods (Fig. S2.6.1). In January –March, the smallest size class was abundant on the reef flat in the *Sargassum ilicifolium* band, indicating that recruitment of this species occurs during the cool months in that particular habitat. Recruits of *S. ferrugineus* are encountered throughout the year, but their proportion is higher during April – June and July – September, contributing to a higher density of this species in April – June. Juveniles of *C. striatus* and *A. gahhm* were rarely seen and their recruitment period or habitat cannot be indicated. However the relative frequency of the 15 – 20 cm size class of both species increased in July – September.

In *S. rivulatus* and *S. ferrugineus* peak density and biomass coincided with the season in which a higher number of recruits were recorded. The fact that recruits of the two surgeonfishes were absent throughout the year and that the 15 – 20 cm fish appear in higher proportions during July – September suggests an ontogenetic habitat shift. Overall roving herbivore biomass was stable throughout the year due to the fact that peak density/biomass of each of these species occurred at different times of the year.

Table S2.6.1 Summary of high tide density (ind. ha^{-1}) and biomass (kg ha^{-1}) estimates of parrotfish, surgeonfishes, rabbitfishes and a rudderfish on four reef zones at Sheikh Said Island fringing reef, southern Red Sea, Eritrea. Numbers are means averaged over four seasons (±SE). The last column refers to density and biomass values averaged over the seasons and four zones.

	Species	Reef flat		Reef crest		Shallow fore reef		Deep fore reef		Reef wide annual average	
		Density	Biomass	Density	Biomass	Density	Biomass	Density	Biomass	Density	Biomass
Acanthuridae	*Acanthurus gahhm*	628.57 (103.32)	203.64 (38.48)	531.71 (75.64)	144.77 (19.41)	153.70 (31.18)	44.99(9.96)	145.45(39.19)	60.17 (18.31)	373.33 (38.96)	114.95 (12.85)
	Ctenochaetus striatus	64.76 (27.80)	9.46 (4.70)	855.28 (44.35)	142.83 (8.60)	396.29 (44.04)	57.64 (8.03)	151.52 (27.71)	24.32 (4.89)	390.34 (32.35)	62.51 (5.65)
	Zebrasoma veliferum	0.0	0.0	74.79 (14.19)	30.39 (6.23)	68.69 (16.28)	17.34 (5.10)	44.44 (16.83)	12.59 (4.97)	47.89 (7.19)	15.78 (2.59)
	Acanthurus sohal	0.0	0.0	94.31 (18.03)	49.98 (9.56)	12.96 (9.51)	4.05 (2.97)	10.10 (6.57)	2.82 (1.75)	32.18 (6.62)	15.78 (3.33)
	Zebrasoma xanthurum						✓	✓			
	Total	**693.33 (109.1)**	**213.10 (39.25)**	**1556.10 (100.96)**	**367.96 (28.92)**	**625.93 (73.28)**	**124.02 (19.07)**	**351.52 (63.71)**	**99.91 (21.42)**	**842.75 (59.22)**	**209.01 (16.72)**
Scaridae	*Scarus ferrugineus*	422.86 (113.57)	111.62 (33.98)	2180.49 (131.19)	571.95 (35.43)	818.52 (80.59)	225.47 (25.97)	501.01 (70.24)	164.46 (25.92)	1035.86 (80.40)	282.07 (21.91)
	Chlorurus sordidus	34.29 (11.05)	5.75 (1.99)	411.38 (47.59)	52.76 (7.20)	164.81 (26.49)	31.27 (5.19)	80.81 (20.87)	14.72 (3.66)	183.91 (20.14)	27.42 (2.99)
	Hipposcarus harid	746.67 (149.47)	184.00 (41.07)	269.92 (67.55)	92.94 (22.14)	94.44 (44.32)	30.93 (15.25)	10.10 (5.13)	2.12 (1.06)	282.29 (47.86)	78.85 (13.45)
	Scarus collana	394.28 (61.47)	59.39 (10.96)	112.19 (25.23)	14.47 (3.27)	151.85 (22.48)	22.93 (3.94)	113.13 (23.11)	20.66 (4.36)	190.34 (20.46)	28.82 (3.42)
	*Scarus niger**					✓	✓				
	*Scarus ghobban**							✓	✓		
	*Bolbometaphon muricatum**							✓	✓		
	*Leptoscarus sps.**	✓	✓								
	*Chlorurus genazonatus**					✓	✓				
	Total	**1598.09 (212.56)**	**360.76 (57.84)**	**2973.98 (180.17)**	**732.12 (45.17)**	**1229.63 (111.19)**	**310.63 (36.39)**	**705.05 (84.34)**	**201.96 (28.59)**	**1692.41 (106.67)**	**417.18 (27.66)**
Siganidae	*Siganus rivulatus*	9447.61 (1309.75)	573.25 (92.14)	2094.31 (319.68)	133.31 (22.02)	1094.44 (328.79)	57.07 (18.88)	80.81 (29.98)	4.91 (2.07)	3162.75 (450.77)	191.35 (29.68)
	*Siganus luridus***	0.0	0.0	78.04 (56.83)	5.34 (3.76)	5.56 (4.09)	0.37 (0.27)	2.02 (2.02)	0.05 (0.05)	23.91 (16.22)	1.61 (1.07)
	*Siganus stellatus***	0.0	0.0	6.50 (4.54)	0.93 (0.65)	7.41 (5.16)	1.06 (0.74)	8.08 (5.62)	0.86 (0.64)	6.20 (2.48)	0.72 (0.30)
	Total	**9447.61 (1309.75)**	**573.25 (92.14)**	**2178.86 (317.27)**	**139.58 (21.94)**	**1107.41 (332.38)**	**58.49 (19.10)**	**90.91 (31.09)**	**5.82 (2.13)**	**3192.18 (450.21)**	**193.68 (29.64)**
*Kyphosus cinerascens***		0.0	0.0	0.0	0.0	18.51 (12.91)	1.73 (1.34)	26.26 (18.34)	3.90 (2.76)	10.57 (5.28)	1.31 (0.71)
All roving herbivores		**11739.05 (1419.92)**	**1147.10 (145.69)**	**6708.94 (399.31)**	**1239.66 (63.95)**	**2981.48 (358.36)**	**494.88 (46.78)**	**1173.74 (129.78)**	**311.58 (42.26)**	**5737.93 (494.24)**	**821.17 (53.56)**

[*] Species that were encountered outside transects. These species, although found in higher abundances on other southern Red Sea reefs, were rare on the study site. The zone on which they were spotted is indicated by a check mark (✓)

[**] Species that were encountered on transects, but were rare. These were not included on the community structure analysis and on the species level patterns of distribution. However they were included on the total density and biomass of roving herbivores.

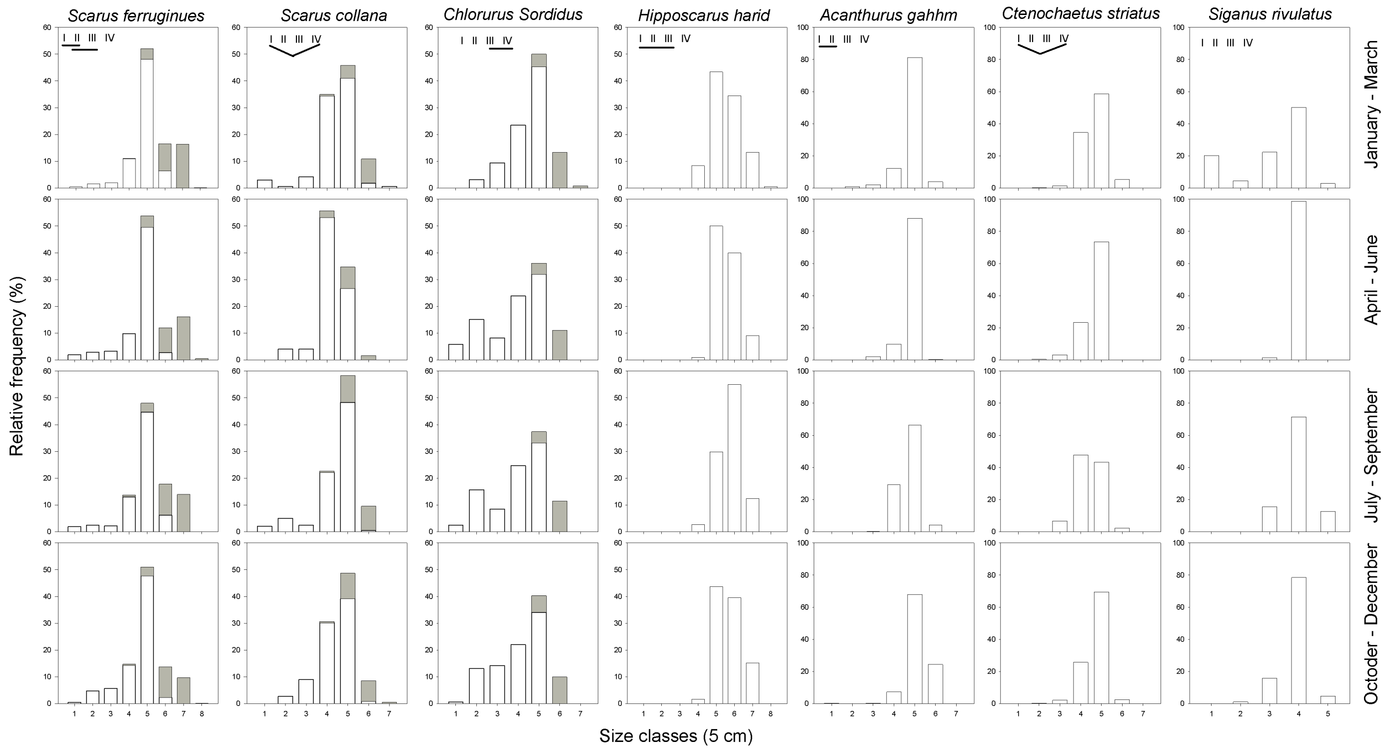

Fig. S2.6.1 Temporal patterns on the size frequency distribution of common roving herbivorous fishes of Sheikh Said Island, the southern Red Sea, Eritrea. I: January – March, II: April – June, III: July – September, IV: October – December. Seasons with similar size structure are underlined or linked with a line. For the three parrotfishes; Initial phase (open bars) and Terminal phase males (grey bars) are indicated.

Table S2.6.2 Total roving herbivore density and biomass. Summary of Repeated Measures ANOVA results of field data collected from fixed transects (n = 6) in four periods during 2006 – 2008. *df*: degrees of freedom, *F*: ANOVA F-statistic, *P*: probability. Significant *P* values in bold type.

Source		Density			Biomass		
		df	*F*	*P*	*df*	*F*	*P*
Period		2.196	3.459	**0.036**	3	1.796	0.158
Zone		3	128.618	**0.000**	3	63.312	**0.000**
Period*Zone		6.588	5.142	**0.000**	9	4.112	**0.000**
SFR	Tide	1	33.564	**0.004**	1	31.135	**0.005**
	Tide*Period	2.048	0.727	0.515	3	2.744	0.089
DFR	Tide	1	69.715	**0.001**	1	10.344	**0.001**
	Tide*Period	1.295	12.895	**0.013**	3	27.694	**0.000**

S2.7 Effect of tide on distribution patterns of roving herbivores

To test the effect of tide on the distribution of roving herbivores, counts were conducted both at high and low tides in the shallow fore reef and deep fore reef (no distinction was made between neap and spring tides). The reef flat and reef crest were surveyed at high tide only because at low tide these become too shallow for snorkelling. Effect of tide on the distribution of total gazer and individual species was investigated by comparing biomass and density between high and low tide at the shallow fore reef and deep fore reef; a two-way RMA, was used with tide and period as repeated measures and zone as between subject factor. When conducting RMA, assumption of sphericity was tested by Maculay's sphericity test and the Greenhouse-Geisser correction was applied when that assumption was violated.

Herbivore density and biomass was affected significantly by the state of tide on the shallow fore reef and deep fore reef (Table S2.6.2). Both zones supported higher density and biomass of herbivores at low tide than at high tide (Fig. S2.7.1). At the shallow fore reef the effect of tide was the same during all periods, while at the deep fore reef the interaction between tide and period was significant (Table S2.6.2). During April – June, the deep fore reef had higher density and biomass at high tide than at low tide, a trend that is opposite to the rest of the periods where high tide values are consistently lower. Species level analysis (see below) shows that this trend is caused by a single species namely *S. ferrugineus*.

Table S2.6.3 Density and biomass of common roving herbivorous fishes at Sheik Said Island fringing reef, southern Red Sea Eritrea. Summary of Repeated Measures ANOVA results of field data collected from fixed transects in four periods during 2006 – 2008. df: degrees of freedom, F: ANOVA F-statistic, P: probability. Significant P values in bold type.

Species	Density									Biomass								
	Zone			Period			Zone*Period			Zone			Period			Zone*Period		
	df	F	P	df	F	P	df	F	P	df	F	P	df	F	P	df	F	P
Acanthurus gahhm	3	40.065	**0.000**	2.201	7.329	**0.001**	6.602	0.436	**0.000**	3	30.666	**0.000**	2.391	10.179	**0.000**	7.173	5.573	**0.000**
Acanthurus sohal	3	56.534	**0.000**	1.953	0.123	0.880	5.860	1.099	0.380	3	105.337	**0.000**	1.884	0.226	0.786	5.651	1.173	0.341
Chlorurus sordidus	3	22.300	**0.000**	2.512	2.577	0.074	7.536	2.761	**0.015**	3	20.206	**0.000**	2.389	0.528	0.625	7.168	2.338	**0.038**
Ctenochaetus striatus	3	100.511	**0.000**	2.342	6.509	**0.002**	7.026	3.381	**0.005**	3	136.162	**0.000**	2.836	4.907	**0.005**	8.507	3.176	**0.004**
Hipposcarus harid	3	27.671	**0.000**	1.877	2.124	0.136	5.631	2.099	0.080	3	22.125	**0.000**	1.893	1.967	0.156	5.680	1.902	0.109
Scarus collana	3	11.609	**0.000**	2.510	1.166	0.327	7.530	6.665	**0.000**	3	10.961	**0.000**	2.686	1.520	0.223	8.059	8.874	**0.000**
Scarus ferrugineus	3	40.753	**0.000**	2.340	4.669	**0.011**	7.020	6.178	**0.000**	3	31.633	**0.000**	2.080	4.869	**0.012**	6.240	5.568	**0.000**
Siganus rivulatus	3	72.721	**0.000**	1.976	3.936	**0.028**	5.927	1.177	0.338	3	50.963	**0.000**	2.099	0.179	0.847	6.298	1.265	0.293
Zebrasoma veliferum	3	14.672	**0.000**	2.594	0.442	0.696	7.782	2.382	**0.033**	3	19.861	**0.000**	2.788	1.951	0.138	8.365	3.128	**0.006**

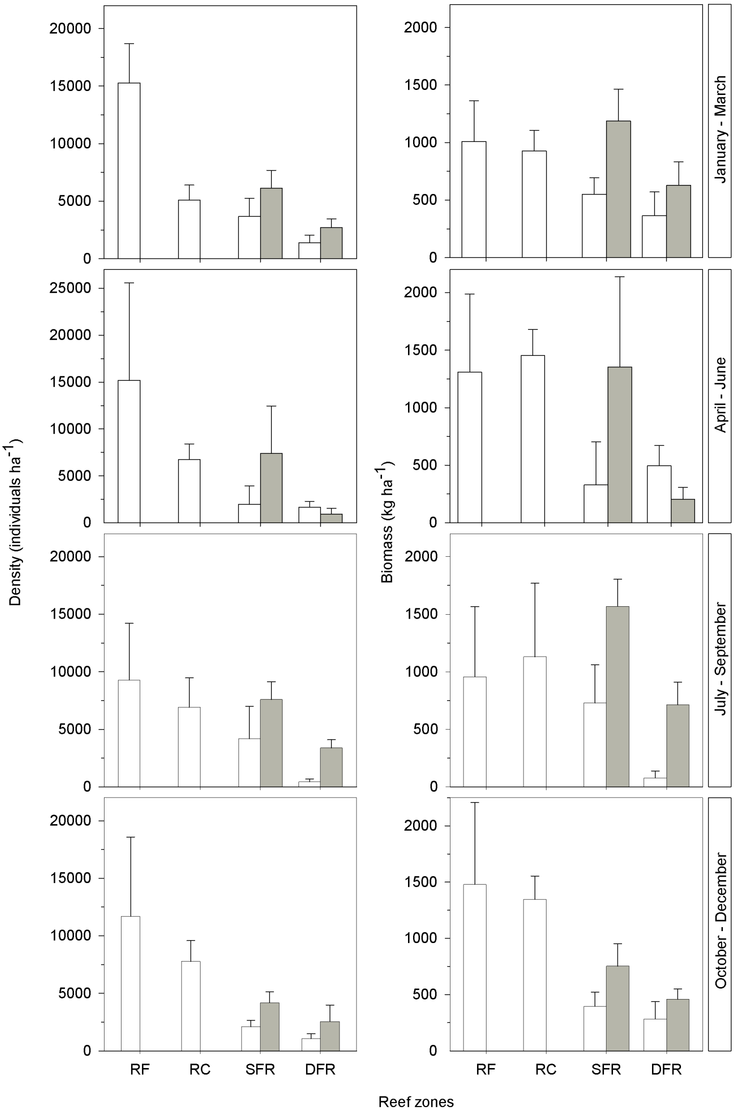

Fig. S2.7.1 Effect of tide on the total density and biomass of roving herbivores in four reef zones during four periods at Sheikh Said Island, southern Red Sea, Eritrea. Bars indicate means and their 95% confidence interval. Open bars: high tide values, grey bars: low tide values.

Table S2.7.1 Density and biomass of common roving herbivorous fishes at Sheik Said Island, southern Red Sea, Eritrea. Summary of Two-way Repeated Measures ANOVA on the effect of tide on density and biomass of roving herbivores. Density/biomass data collected from fixed transects in four periods during 2006 – 2008. *df*: degrees of freedom, *F*: ANOVA F-statistic, *P*: probability. Significant *P* values in bold type.

	Species	Tide			Tide*Zone			Tide*Period		
		df	*F*	*P*	*df*	*F*	*P*	*df*	*F*	*P*
Density	*Acanthurus gahhm*	1	49.836	**0.000**	1	4.877	0.058	1.516	2.643	0.120
	Acanthurus sohal	1	0.587	0.466	1	4.668	0.063	2.152	0.873	0.443
	Chlorurus sordidus	1	9.621	**0.015**	1	4.261	0.073	1.963	0.606	0.555
	Ctenochaetus striatus	1	0.593	0.463	1	0.438	0.527	2.172	2.204	0.137
	Hipposcarus harid	1	108.810	**0.000**	1	0.073	0.794	2.368	1.951	0.165
	Scarus collana	1	28.466	**0.001**	1	0.063	0.808	2.247	1.434	0.265
	Scarus ferrugineus	1	37.790	**0.000**	1	1.738	0.224	2.092	7.999	**0.003**
	Siganus rivulatus	1	28.769	**0.001**	1	0.130	0.728	2.399	1.173	0.338
	Zebrasoma veliferum	1	0.937	0.370	1	1.182	0.319	2.352	1.058	0.383
Biomass	*Acanthurus gahhm*	1	42.516	**0.000**	1	2.812	0.132	1.596	2.356	0.141
	Acanthurus sohal	1	0.949	0.359	1	4.282	0.072	2.063	0.840	0.453
	Chlorurus sordidus	1	6.449	**0.035**	1	4.772	0.060	1.985	0.169	0.845
	Ctenochaetus striatus	1	4.063	0.079	1	1.268	0.293	2.428	1.785	0.190
	Hipposcarus harid	1	63.958	**0.000**	1	0.051	0.826	2.080	1.045	0.376
	Scarus collana	1	33.833	**0.000**	1	1.710	0.227	2.386	2.823	0.077
	Scarus ferrugineus	1	51.168	**0.000**	1	42.387	**0.000**	1.931	6.639	**0.009**
	Siganus rivulatus	1	19.387	**0.002**	1	19.387	**0.002**	1	1.278	0.291

Species level tests indicated the existence of two groups of herbivores (Table S2.7.1), those that show significantly higher density and biomass on the shallow fore reef and deep fore reef at low tide than at high tide (Fig. S2.7.2) and those which do not. Members of the first group migrate at high tide to the reef crest (*C. sordidus* and *S. ferrugineus*) and the reef flat (*A. gahhm*, *H. harid*, *S. collana*, and *S. rivulatus*). The second group, comprising the three surgeonfish species *A. sohal*, *C. striatus* and *Z. veliferum*, did not show significant tide-related shifts in distribution. For all species effecting tidal distribution shifts, with the exception of *S. ferrugineus* and *S. rivulatus*, the effect of tide was the same for the shallow fore reef and deep fore reef (no significant tide x zone interaction) and this effect remained the same throughout the year (no significant period* tide interaction). In *S. rivulatus* the effect of tide was significant only for the shallow fore reef. Apparently this species does not descend to the deep fore reef at low tide. In *S. ferrugineus* the effect of tide on density/biomass concurs with that in other species, except for the periods January – March and April – June on the deep fore reef. For these periods tide has either no effect on density (January – March) or the opposite effect (April – June) (Fig. S2.7.1). This is likely to happen if counting coincided with spawning aggregations of *S. ferrugineus* which take place at the deep fore reef around high tide (see Chapter 7).

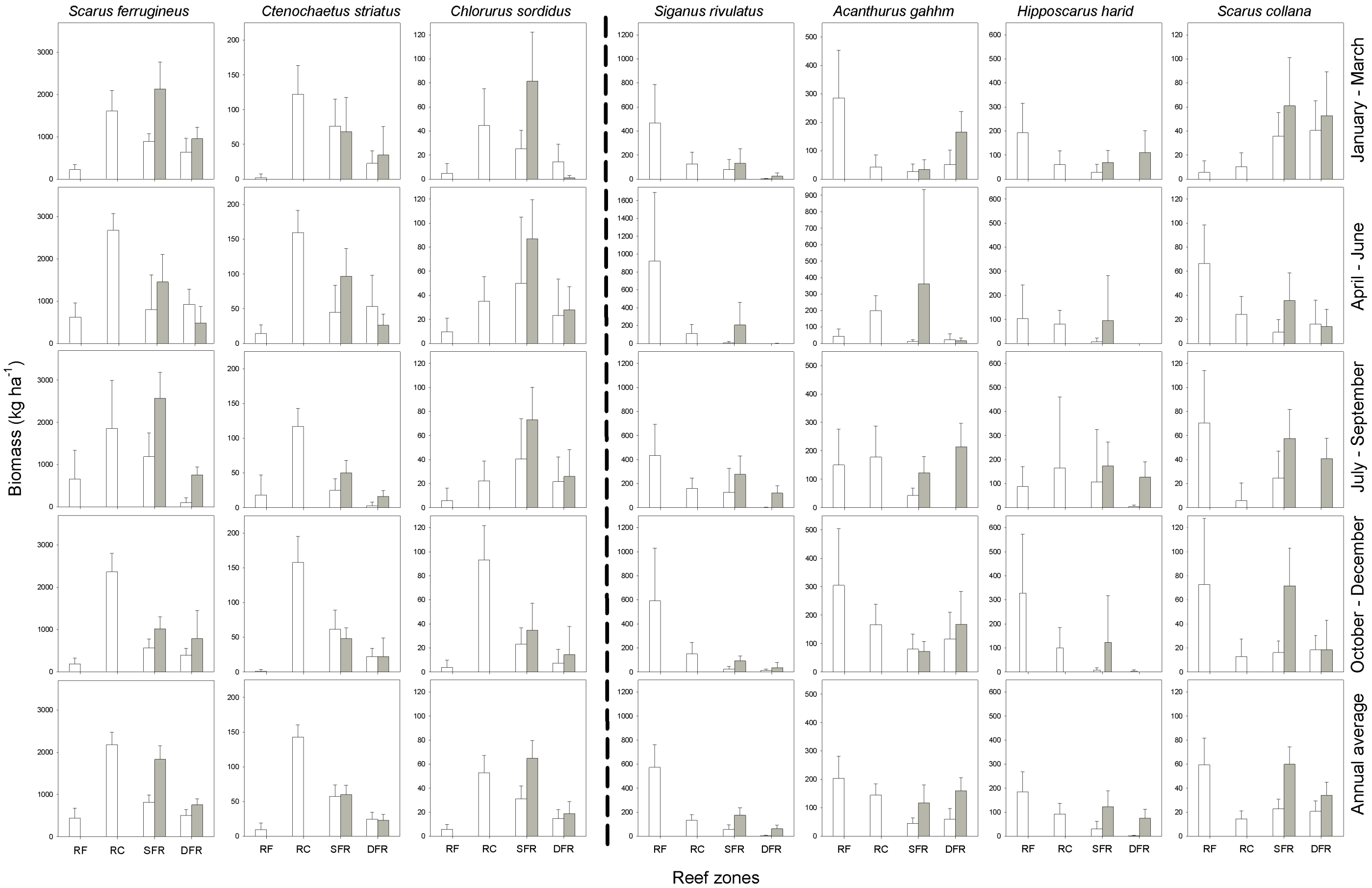

Fig. S2.7.2 Effect of tide on the distribution of roving herbivores on the fringing reef of Sheikh Said Island, southern Red Sea. Annual average values of biomass are given in the bottom set of graphs. Broken line separates the two groups of species that characterize the reef crest (left three sets) and the reef flat (right four sets). Bars represent means with 95% confidence interval; open bars: high tide values, grey bars: low tide values.

The tide-associated migrations between reef zones resulted in biomass differences between high and low tide in the order of 200 to 300% (see Fig. S2.7.1 and Fig. S2.7.2) in particular at the shallow fore reef. This highlights the importance of tide in structuring the distribution of coral reef fishes. Ignoring tide as a factor in underwater census will introduce a large variation in fish counts making it difficult to detect actual changes in populations. It is therefore imperative, as Thompson and Mapstone (2002) have argued, that reef fish monitoring efforts should control for tide if accurate estimates are to be made. To minimize this tide associated variation, in this study only high tide counts were used to compare patterns in habitat use.

S2.8 Relative biomass of roving herbivore functional groups

The proportion of total biomass represented by the different functional groups in each reef zone is shown for the different periods.

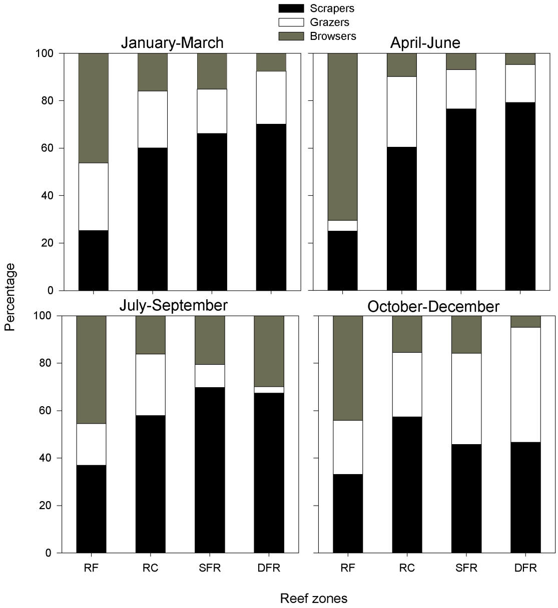

Fig. S2.8.1 Seasonal trends in the percentage composition of three functional groups of roving herbivores at four reef zones in a fringing reef at Sheikh Said Island, southern Red Sea, Eritrea. RF: reef flat; RC: reef crest; SFR: shallow fore reef; DFR: deep fore reef.

CHAPTER 3

LIMITED FLEXIBILITY IN RESOURCE USE IN A CORAL REEF GRAZER FORAGING ON SEASONALLY CHANGING ALGAL COMMUNITIES

Y. Afeworki, J. H. Bruggemann, & J.J. Videler

Abstract Feeding ecology of three life phases of the parrotfish *Scarus ferrugineus* was studied on a southern Red Sea fringing reef by comparing availability and consumption of benthic algae during the monsoon hot and cool seasons. Dominant biota covering dead carbonate substrates were in decreasing order of importance: turfs on endoliths, turfs on crustose corallines, and crustose corallines. On the reef crest and shallow fore reef composition of the bota changed seasonally. Cover of turfs on endoliths and turfs on crustose corallines was higher during the hot season, while crustose corallines and macroalgae (only on reef crest) increased during the cool season. Biota in the deep fore reef did not show seasonal variation. All life phases used similar resources and showed selective feeding in all zones. Turfs on endoliths followed by turfs on crustose corallines was the primary feeding substrate. These two sources represented over 92% of bites during both seasons. Crustose corallines, macroalgae and living corals were negligible components being strongly avoided at all zones and seasons. Resource use varied seasonally on the reef crest and shallow fore reef, while it remained unchanged on the deep fore reef. Turfs on endoliths were consistently preferred in both seasons but their contribution increased from 45% in the cool to 70% of bites in the hot season. Electivity for turfs on crustose corallines shifted from random feeding in the hot (27% of bites) to selection in the cool season (47% of bites). Feeding pattern changed diurnally with more bites taken from crustose corallines and turfs on crustose corallines during morning. During the rest of the day bites from turfs on endoliths predominate. *S. ferrugineus* shows limited capacity to exploit seasonal increases in biomass of foliose and canopy forming macroalgae, despite indications of energetic limitation during the cool season.

Coral reefs (2011) 30:109–122

3.1 Introduction

Herbivorous fishes have long been recognized as a major force structuring benthic communities on coral reefs (Randall 1961; Hay et al. 1983; McClanahan et al. 2003; Burkepile & Hay 2009). Parrotfishes (family Labridae) are probably among the most important components of the grazing guild owing to their high biomass and wide distribution and a feeding mechanism that is highly specialized for scraping algae and detritus from carbonate substrates (Russ 1984a; Choat 1991; Fox & Bellwood 2007; Mumby et al. 2007; Sotka & Hay 2009). Within this family, species differ in their feeding mode (for example excavator vs scraper), microhabitat use, and food selection (Bellwood & Choat 1990; Bruggemann et al. 1994a; Hoey & Bellwood 2008). Also size determines the functional role of a species, which changes during ontogeny (Bonaldo & Bellwood 2008; Lokrantz et al. 2008). Assessment of the impact of scarids on coral reef benthic communities therefore requires a detailed analysis of their feeding ecology, not only at the species level but also among the different size and life-history stages of each species (Bellwood et al. 2003; Bonaldo & Bellwood 2008; Burkepile & Hay 2008).

Coral reefs are not restricted to oligothrophic, temporally stable oceanic environments (Hatcher 1997). Many coral reefs thrive in upwelling areas and in seasonal seas where significant temporal changes in benthic algal community are typical (Diaz-Pulido & Garzon-Ferreira 2002; Ateweberhan et al. 2006a). Such areas offer unique situations to study responses of grazers to the changing biotic and abiotic conditions. Despite this, the effect of seasonally changing food supply on the ecology of scarids has not been studied extensively (Lefevre & Bellwood 2010). A notable exception is the detailed work of Clifton (1995) who reported significant changes in reproduction and growth of *Scarus iserti* in Panama as a consequence of changes in the productivity of turf algae.

The southern Red Sea is characterized by monsoon associated seasonal fluctuations in environmental conditions with high temperatures in summer (Edwards 1987). The resulting seasonal changes in the biomass and cover of algal functional groups (Ateweberhan et al. 2006a) are reminiscent of winter-spring shifts in biomass of temperate rocky shores (Murray & Horn 1989; Gunnarsson & Ingolfsson 1995). This setting makes the fringing reefs of the southern Red Sea an ideal environment to investigate the effects of extreme temperatures and seasonality on grazing and its role in mediating the interaction between algae and corals.

We present here results on the feeding ecology of different life phases of the endemic *Scarus ferrugineus* in relation to seasonal changes in algal functional groups, studied on a fringing reef in the southern Red Sea. This species is the dominant parrotfish in the area. Despite its potentially important ecological role, virtually nothing is known of the biology of this species. Specific questions we sought to answer were: How do different life phases of *S. ferrugineus* use benthic resources in different reef zones? Does the seasonal change in the availability of algal functional groups affect the feeding preference of the species?

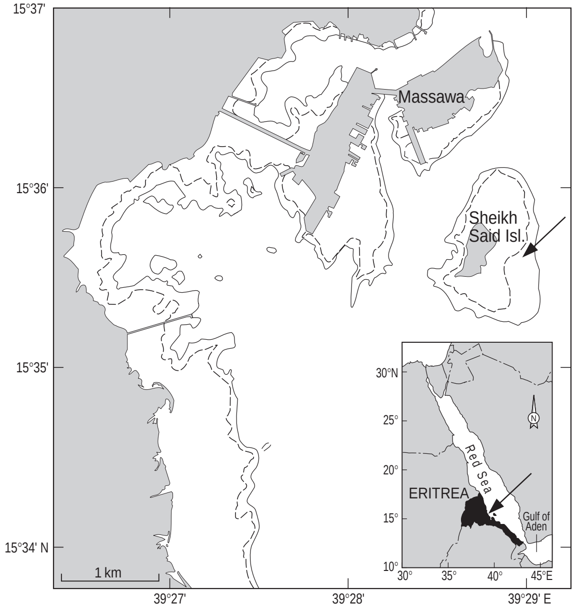

Fig. 3.1 Map of Massawa (Eritrea), southern Red Sea, showing Sheikh Said Island (arrow). Figure by Dick Visser.

3.2 Materials and methods

3.2.1 Study site

The study was conducted between January 2006 and April 2008 on a fringing reef at the windward side of Sheikh Said Island near Massawa, Eritrea (15°35′N; 39°29′E) (Fig. 3.1). Four reef zones with distinct morphologies were identified: the reef flat, the reef crest, the shallow fore reef and the deep fore reef. The reef flat is a 40 – 55 m wide subtidal zone (0 – 1 m deep), mainly composed of consolidated limestone pavement and loose coral rubble. The reef flat as it is defined here comprises the inner, middle and part of the outer reef flats described by Ateweberhan et al. (2006a). During the cool season, this area is covered by dense growths of *Sargassum illicifolium* on the landward side and by open stands of *Turbinaria triquetra* along the seaward margin. The reef crest (0 to 2 m deep) is a transition zone between the reef flat and the shallow fore reef, and is partly exposed during extreme low tides. The substrate on the landward side is composed of limestone pavement and loose coral rubble. The deeper side of the reef crest is largely covered by living and dead corals, mainly *Porites* and *Montipora*. The shallow fore reef, (2 – 6 m deep), is characterized by large colonies of massive *Porites* scattered in a zone dominated by sand and rubble. Encrusting *Echinopora* corals are abundant on the shallower part of this zone. The deep fore reef (6 – 10 m depth) has the highest coral cover dominated by *Lobophylia* and *Echinopora*. In its deepest part, the soft coral *Xenia* covers much of the bottom surface down to a depth of 13 m. Deeper down coral growth is absent giving way to a gently sloping sandy expanse.

The study site is in a good condition with minimal fishing activity restricted to few canoe fishermen targeting predatory fishes. The absence of spear fishing permits behavioural observations at close range.

3.2.2 Environmental conditions

The southern Red Sea experiences significant monsoon associated changes in environmental conditions (Edwards 1987). Two distinct seasons are identifiable: a cool season that extends from November to April which is associated with the north-eastern monsoon, and a hot season spanning May to October and associated with the south-western monsoon (Ateweberhan et al. 2006b). At the study site, mean monthly water temperatures at 2 m depth range from 27.7°C during the cool to 33.4°C in the hot season (Ateweberhan et al. 2006a). This is associated with significant changes in the composition and biomass of the benthic algae (Ateweberhan et al. 2006a). Briefly stated, the cool season is characterized by the building-up of large stands of foliose and canopy forming macroalgae in the reef flat and parts of the reef crest, and high biomass of crustose corallines in the reef crest and shallow fore reef. The hot season induces significant reduction in cover and biomass of macroalgae and crustose corallines while turf algae increase.

3.2.3 Study animal

The rusty parrotfish *Scarus ferrugineus* Forsskål, 1775 is a member of the family Labridae, endemic to the Red Sea and the Arabian Sea, and a dominant scarid on the reefs of the southern Red Sea. It is a diandric protogynous hermaphrodite (Randall & Ormond 1978). The Terminal Phase males (TP) are colourful with shades of green, yellow and pink and dominate the large size classes. The Initial Phase (IP) fish are reddish-brown to brown and comprise the smaller size classes. At the study site maximum size recorded for TP fish is 36 cm while the IP fish reach 26 cm.

3.2.4 Habitat description

Surveys of available substrates and potential food sources were made during the peaks of cool (January to March) and hot (July to September) seasons. Relative abundance of substrates and algal vegetation types of the reef crest, shallow fore reef and deep fore reef zones was determined using chain-link transects (Bruggemann et al. 1994b). The reef flat was excluded as our visual surveys indicated very low numbers of *Scarus ferrugineus* in this zone.

In each zone, a 99 m long line transect was laid parallel to the coast at a haphazardly selected location and fixed with metal stakes at intervals of 30 m. This transect provided the backbone of two parallel grids of 33 squares (3 m x 3 m) on either side (see Appendix 3.1). Each of the 66 quadrats was allocated a unique number of which 20 were randomly selected as permanent sampling locations for both the cool and hot seasons.

At each selected quadrat, two 3 m long chains of 150 links each were laid out along two sides of the selected quadrat, parallel and perpendicular to the shore and following the contours of the substrate. The substrate type and biota under (the welding point of) each chain link was determined visually. The following substrate categories were used: living coral, dead coral, coral rubble, limestone pavement and sand. Living corals were identified to genus level. Where possible, the origin of dead coral substrates was also identified to genus level. Moreover, the orientation of dead coral substrate was differentiated as: horizontal, edge, vertical, overhanging and coral base.

The biota growing in or on dead coral, coral rubble and limestone pavement was classified following Bruggemann et al. (1994b) as: turfs growing on endolithic algae (henceforth turfs on endoliths), turfs growing on crustose coralline algae (henceforth turfs on crustose corallines), bare crustose coralline algae, turfs growing on boring sponges (henceforth turfs on sponges), invertebrates other than corals (henceforth invertebrates) or macroalgae.

3.2.5 Bite description

Feeding behaviour of *Scarus ferrugineus* was recorded within the marked transects and in approximately the same periods during which the benthic surveys were made. A haphazardly selected fish was allowed to acclimate to the observer for 3 minutes during which time the life phase, fork length, time of day and the approximate location were recorded. Only one bite was described per fish. Resampling of individual fish was minimized by swimming away from the area where the last bite was described before selecting another fish. Moreover, the large population size of the species at the study site makes resampling of the same individual unlikely.

To ensure random sampling of bites, a number between 5 and 15 was randomly selected before each dive to represent the n^{th} bite to be described. The exact location of the n^{th} bite was spotted and the nature of the substrate, its orientation and the biota covering it noted. Moreover, the microtopography (convex, flat, concave), scar production and the 'foray' length (sensu Bellwood & Choat 1990) were recorded.

Possible diurnal change in resource use was investigated by sampling bites during the morning (0600 hrs – 1100 hrs), around noon (1100 hrs – 1300 hrs) and in the afternoon (1300 hrs – 1800 hrs). All field work was conducted by the same observer (Y.A.).

3.2.6 Statistical analysis

Multivariate tests of similarity (ANOSIM) were used to compare the composition of substrates, live coral genera and biota between the seasons in each zone and among zones in each season. Whenever the differences are significant, the contribution of categories to the average dissimilarity was assessed based on similarity percentage analysis (SIMPER). SIMPER and ANOSIM tests were conducted using PRIMER-E v5.2 (Clarke & Warwick 2001).

Correspondence analysis was used to assess the degree of association between the orientation of dead coral substrate parts and the biota covering it. Life phase related differences in resource utilization were studied, controlling for zone and season, at the level of substrate, food (biota) and dead coral genera using two-way contingency tables followed by chi-square tests. Differences in feeding between the seasons and day times were compared similarly using chi-square.

Selection of grazing substrates, biota and dead coral types was tested by comparing their utilisation to availability in each zone and season using chi-square tests. Preference was analysed using Ivlev's electivity index (Equation 3.1) (Lechowicz 1982). Values for Ivlev's index range from -1 (avoidance) to 1 (preference). Zero indicates random feeding. Bootstrapping procedure (300 simulations) was conducted on individual bites (keeping resource abundance constant (Smith 1982)) to estimate confidence limits of electivity values. Ivlev's electivity values were tested against random feeding by looking if the confidence interval included zero or not.

$$E = \frac{r_i - p_i}{r_i + p_i} \qquad (3.1) \qquad\qquad B' = \frac{1}{\sum_{i=1}^{R}(p_i^2/q_i)} \qquad (3.2)$$

Niche breadth was estimated using the weighted version of Levin's measure (Equation 3.2) (Hurlbert 1978). For calculation of niche breadth, all potential food sources in the habitat were considered. This measure can take values between 0 (specialist feeder) and 1 (generalist feeder). Seasonal difference in niche breadth was tested using Z-test (Smith 1982).

Resource selection was further investigated using foray lengths, assuming that longer forays are indicators of preference (Bruggemann et al. 1994b). Forays were classified into nine classes of 1-3, 4-6, 7-9, 10-12, 13-15, 16-18, 19-21, 22-24, >25 bites. Differences in frequency distribution of forays for the different biota items were then tested by chi-square tests controlling for life phase, season and zone. Difference in scar production – expressed as the percentage of total bites producing visible grazing scars - among life phases was analysed by ANCOVA, taking percentage of scars as a dependent variable, life phase as a fixed factor and fish fork length as a covariate.

Whenever some cells in the contingency tables contained very low expected frequencies they were grouped together and Fisher's exact test (FET) was used instead of chi-square. All chi-square, ANCOVA, and correspondence tests were conducted on SPSS for Windows v 16.0 (2007).

3.3 Results

3.3.1 Substrate composition

A total of 29,390 chain link points were described during this study (Appendix A3.3). To compare zones, seasonal substrate composition data was pooled since these did not differ (ANOSIM: Global-r = 0.066, -0.029 and -0.069, P = 0.061, 0.852 and 0.974, for the reef crest, shallow fore reef and deep fore reef respectively). Substrate composition was significantly different among the zones (ANOSIM: Global-r = 0.351, P = 0.001) and between each pair of zones (ANOSIM: Global-r = 0.347 to 0.373, and P = 0.001 in each case). Primary contributors (SIMPER) to this difference were the high living coral cover in the deep fore reef, the large cover of sandy areas in the shallow fore reef and the high extent of limestone pavement in the reef crest. Among the three zones, the reef crest has the largest proportion of the substrates suitable for algal growth and hence for parrotfish grazing. There, the sum of cover by coral rubble, dead coral and limestone pavement is 61%. This figure is 50% on the shallow for reef and 32% on the deep fore reef.

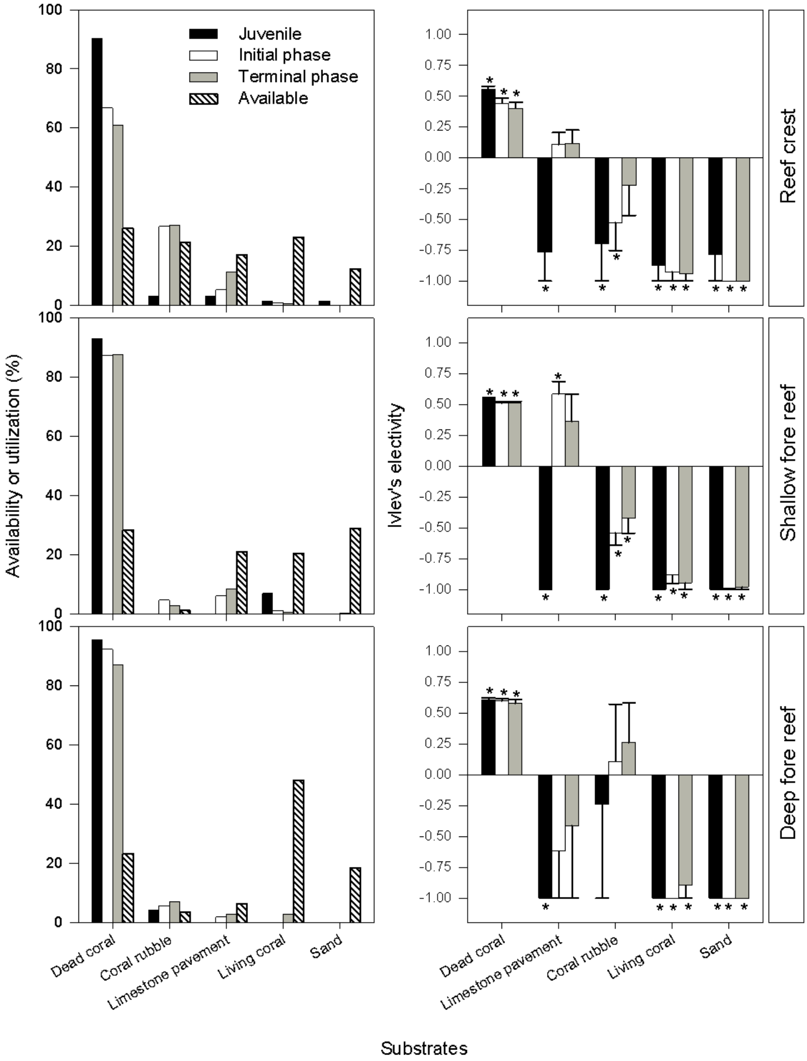

Fig. 3.2 *Scarus ferrugineus*. Availability and utilization (left) and electivity (right) of the major substrate categories by life phase and reef zones. Bars are bootstrap generated 95% confidence intervals. Asterisks indicate significant difference from random feeding.

Twenty-one coral genera were identified. The deep fore reef had the highest generic richness with 21 genera followed by the shallow fore reef and the reef crest with 19 and 9 genera respectively. Generic diversity based on Jaccard's index was highest on the deep fore reef

(0.6644) followed by shallow fore reef (0.5491) and reef crest (0.4889). Coral community composition among zones was compared by pooling seasonal data as there was no difference between the seasons (ANOSIM: Global-r = -0.015, -0.049 and 0.056, P = 0.583, 0.986 and 0.114 for reef crest, shallow fore reef and deep fore reef respectively). Coral composition was significantly different among zones (ANOSIM: Global-r = 0.505, P = 0.001) and all pair wise tests were also significant (ANOSIM: Global-r = 0.208 to 0.794, P = 0.001 in each case). The primary contributors to this difference were the four dominant coral genera: *Porites*, *Echinopora*, *Lobophyllia* and *Montipora*. *Montipora* and *Porites* are characteristic of the reef crest, *Porites* and *Echinopora* of the shallow fore reef and *Lobophyllia* and *Echinopora* of the deep fore reef. All coral genera contributed to the pool of dead coral substrates in direct proportion to their abundances in their living form. This is confirmed by a significant positive correlation between the cover by dead and living coral of each genera.

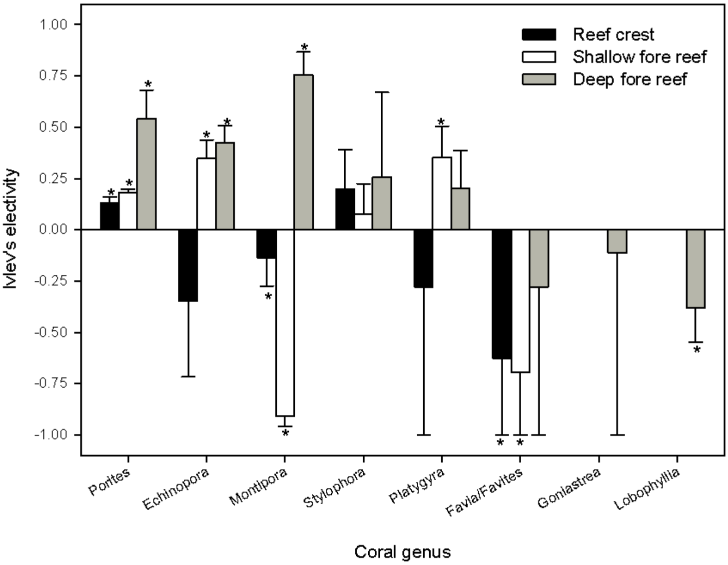

Fig. 3.3 *Scarus ferrugineus*. Selection of dead coral substrates by coral genus and reef zone. Bars are bootstrap generated 95% confidence intervals. Asterisks indicate significant difference from random feeding.

3.3.2 Composition of biota growing on limestone substrates

The most abundant categories of biota were turfs on crustose corallines, turfs on endoliths, and crustose corallines occupying respectively 27 – 51%, 24 – 45% and 12 – 38% of hard substrates, depending on season. The highest cover of macroalgae was 9.8% recorded on the reef crest during the cool season. Invertebrates attained a cover of 10% on the deep fore reef while they were nearly absent in the reef crest and the shallow fore reef (Fig. 3.5 and Appendix A3.4).

Percentage composition of the biota was significantly different between the seasons in the reef crest and shallow fore reef (ANOSIM: reef crest: Global-r = 0.266, *P* = 0.001; shallow fore reef: Global-r = 0.194, *P* = 0.001). The primary cause of this difference is the significant increase in cover of crustose corallines and a corresponding decline in turfs on crustose corallines and turfs on endoliths during the cool season (Fig. 3.5). In the reef crest increase in cover of macroalgae from 0.7 to 10% contributes about 12% of the dissimilarity between the seasons. Biota in the deep fore reef remained unchanged in the course of the year (ANOSIM: Global-r = -0.044, *P* = 0.76).

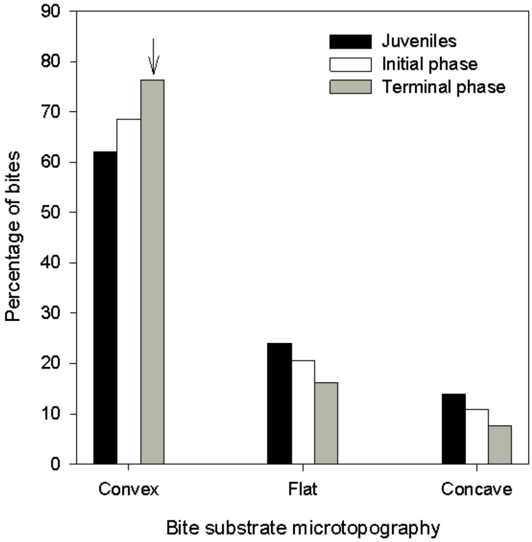

Fig. 3.4 *Scarus ferrugineus*. Use of substrates with different microtopography by each life phase. Arrow indicates that TP use convex surfaces significantly higher than juvenile and IP.

Biota were not randomly distributed across dead coral surfaces with different orientation (correspondence analysis: *P* = 0.000), although substrate orientation explained only 14.6% of the variation in biota composition. About 97.4% of this variation was explained by both the first (91.4%) and the second axis (6%) (Appendix A3.2). Briefly stated, crustose corallines are mainly associated with coral bases and overhanging surfaces, while turfs on endoliths are highly associated with exposed horizontal surfaces. Vertical surfaces were largely covered by turfs on crustose corallines and invertebrates. Patterns of feeding in space and time

3.3.3 Substrate choice

A total of 1606 bites were described, 645 during the cool and 961 during the hot season (Appendix A3.4). Dead corals are the most used feeding substrates for all the life phases of *Scarus*

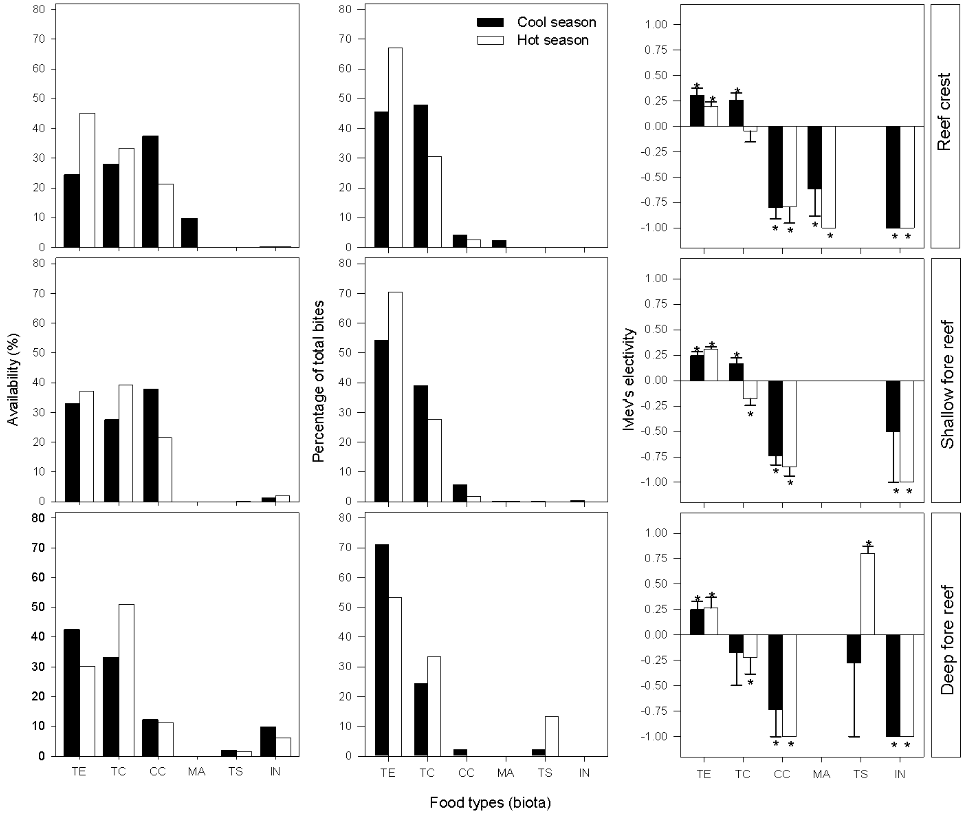

Fig. 3.5 *Scarus ferrugineus.* Availability (left), utilisation (centre) and electivity (right) of the major biota at different reef zones and two seasons. Bars are bootstrap generated 95% confidence intervals. Asterisks indicate significant difference from random feeding. TE: turfs on endolithic algae, TC: turfs on crustose corallines, CC: crustose corallines, MA: macroalgae, TS: turfs on sponge, IN: invertebrates.

ferrugineus (Fig. 3.2), being the target of 83% of bites in IP fish, 80% in TP fish and 92% in juveniles. Limestone pavement sustaining 8.9% and coral rubble sustaining 6.9% of bites are the second - and third-most exploited substrates. Bites from living corals and sand represented 1.2% and 0.2% of total recorded bites respectively.

All life phases showed preference for certain substrates, indicated by the significant difference between utilized and available substrates (χ^2 = 46.78 – 638.51, P = 0.000, df = 4 for all life phases in each zone). Electivity indices show that dead coral is highly preferred (Fig. 3.2). Limestone pavement is used by TP and IP fish at random, although IP fish show preference for this substrate on the shallow fore reef. Living corals and sand are strongly avoided. Coral rubble is avoided in both the shallow fore reef and reef crest zones, while it is used at random in deep fore reef zone.

Utilization of dead coral genera did not differ among life phases or between seasons. Hence, selectivity tests within each zone were conducted by pooling data from life phases and seasons. *S. ferrugineus* is highly selective regarding dead coral substrates (reef crest: $\chi^2 = 38.48$, $df = 5$, $P = 0.000$; shallow fore reef: $\chi^2 = 253.93$, $df = 14$, $P = 0.000$; deep fore reef: $\chi^2 = 92.75$, $df = 15$, $P = 0.000$). Dead *Porites* substrates were the most targeted feeding substrates. In the reef crest and shallow fore reef zones, bites on this substrate constituted 80% of the total. On the deep fore reef, most bites were taken from dead *Echinopora* (43%) and *Porites* (15%) colonies. Ivlev's electivity was calculated for the common genera (Fig. 3.3). Dead *Porites* substrates are consistently preferred in all three zones irrespective of their availability. *Echinopora* is avoided in the reef crest while it is preferred in the shallow fore reef and deep fore reef zones. All other dead coral substrates are either avoided or used in equal proportion to their occurrence, except for *Montipora* in the deep fore reef and *Platygyra* in the shallow fore reef were these substrates were preferred.

Regarding substrate microtopography, all life phases of *S. ferrugineus* took most bites from convex surfaces (Fig. 3.4). TP targeted these significantly more than IP or juvenile fish (χ^2: $df = 4$, $P = 0.027$).

3.3.4 Choice of biota

Analysis of food choice was restricted to the biota growing on dead limestone substrates. Bites on living corals and sand were excluded owing to their low percentage contribution.

Utilisation of biota did not differ among life phases in both seasons and in each of the three reef zones (Appendix A3.4). Therefore, data from life phases was pooled for testing selectivity in each zone and season. Utilization of biota by *S. ferrugineus* was significantly different between seasons on the reef crest and the shallow fore reef (FET: reef crest: 18.247, $P = 0.000$; shallow fore reef: 30.778, $P = 0.000$; Fig. 3.5). Standardized residuals of the chi-square test indicated that a significantly higher utilisation of turfs on endoliths during the hot season was the primary cause of this difference. Moreover, analysis of percentage dissimilarity (SIMPER) indicated that turfs on endoliths followed by turfs on crustose corallines - both food types contributing to over 85% of the dissimilarity - are the primary causes of this seasonal difference. On the deep fore reef there was no seasonal difference in utilization (FET: 2.503, $P = 0.286$).

During each season and in each zone, exploitation of food resources was significantly different from their occurrence (Appendix A3.4), indicating that *S. ferrugineus* is a selective feeder. Ivlev's electivity values (Fig. 3.5) show that turfs on endoliths are preferred in each season and zone. Electivity for turfs on crustose corallines shifted from avoidance on the shallow fore reef and random feeding on the reef crest during the hot season to significant preference during the cool season (Fig. 3.5). In the deep fore reef, turfs on crustose corallines were either avoided (hot season) or used in proportion to their occurrence (cool season). Here, the rare combination of turfs growing on boring sponges were grazed preferentially in the hot season while it was used at random during the cool season. All other potential food items were avoided in all zones during both seasons. The seasonal change in utilization parallels the concomitant change in the availability of the two main food items. Lower cover in turfs on

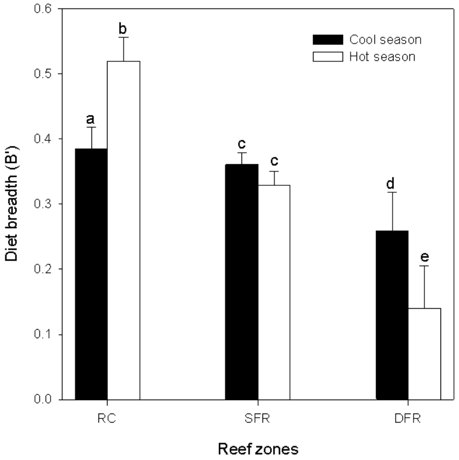

Fig. 3.6 *Scarus ferrugineus.* Feeding niche breadth of adult fish by reef zone and season. Different letters above bars indicate significant seasonal difference within each zone.

endoliths - the main food item - during the cool season leads to an increased inclusion of turfs on crustose corallines from around 30% in the hot to 47% in the cool season. This corresponds to a decline in utilization of turfs on endoliths from around 70% in the hot to 54% the cool season.

Values of the niche breadth ranged from a minimum of 0.16 during the hot season on the deep fore reef to a maximum of 0.53 during the hot season on the reef crest (Fig. 3.6). Overall, *S. ferrugineus* is a specialist feeder in all zones and seasons. Niche breadth is narrowest in the deep fore reef where the resource space is principally occupied by living corals, and it is widest in the reef crest where the preferred food items are more abundant. In the shallow fore reef there was no seasonal difference in niche breadth. In the reef crest, *S. ferrugineus* has a significantly broader feeding niche in the hot compared to the cool season. The opposite is observed in the deep fore reef zone.

3.3.5 Foray size as indicator of feeding preference

Recorded foray lengths ranged from 1 to 35 bites. Data from seasons, life phases and zones was pooled since these did not affect foray size class distribution (FSCD). There was a significant difference in FSCD among biota (FET: 105.204, *P* = 0.001). Stepwise exclusion procedure revealed that the cause of the significance were turfs on endoliths and turfs on crustose corallines. With the exclusion of these two food types, FSCD of the remaining biota are not different among each other (FET: 40.412, *P* = 0.165). The less preferred biota (see above) such as crustose corallines, macroalgae, and invertebrates were characterized by short forays, ranging 1 – 9 bites. On the other hand, turfs on endoliths and turfs on crustose corallines were characterized by longer forays. A closer examination of these two main food types was done for each life phase separately.

For IP and TP fish, the FSCD of turfs on endoliths is highly skewed to the right indicating the prevalence of longer forays (Fig. 3.7) on this food type compared to those taken from turfs on crustose corallines (FET: IP: 15.272, *P* = 0.034; TP: 16.589, *P* = 0.019). For juveniles, the difference between these two food types was not significant (FET: 3.681, *P* = 0.312).

3.3.6 Diurnal changes in food choice

Comparison of biota and surface choice among three periods of the day was done for IP and TP fish alone, as not enough morning bites were recorded for juveniles. Biota selection by IP and TP fish was similar for each period of day; therefore data from both life phases was pooled for subsequent tests. During the morning choice of biota was similar in both the cool and hot seasons (FET: 7.885, *P* = 0.129). In contrast, it varied significantly with season for noon and afternoon periods – parts of the day when the bulk of the bites are taken (FET: noon: 10.352, *P* = 0.014; afternoon: 15.092, *P* = 0.009); diurnal changes in resource use were therefore analysed for each season separately.

For each season, biota choice differed significantly among daytime periods (FET: cool season: 47.778, *P* = 0.000; hot season: 13.904, *P* = 0.019; Fig. 3.8). Stepwise elimination procedure revealed that resource use in the morning is significantly different from the other two periods of day, which were not different from each other. In general, during the morning more bites were taken from less preferred food types such as turfs on crustose corallines and crustose corallines. During noon and afternoon the majority of bites are taken from turfs on endoliths.

Similarly, choice of feeding surfaces was significantly different among the three periods of day in both seasons (FET: cool season:

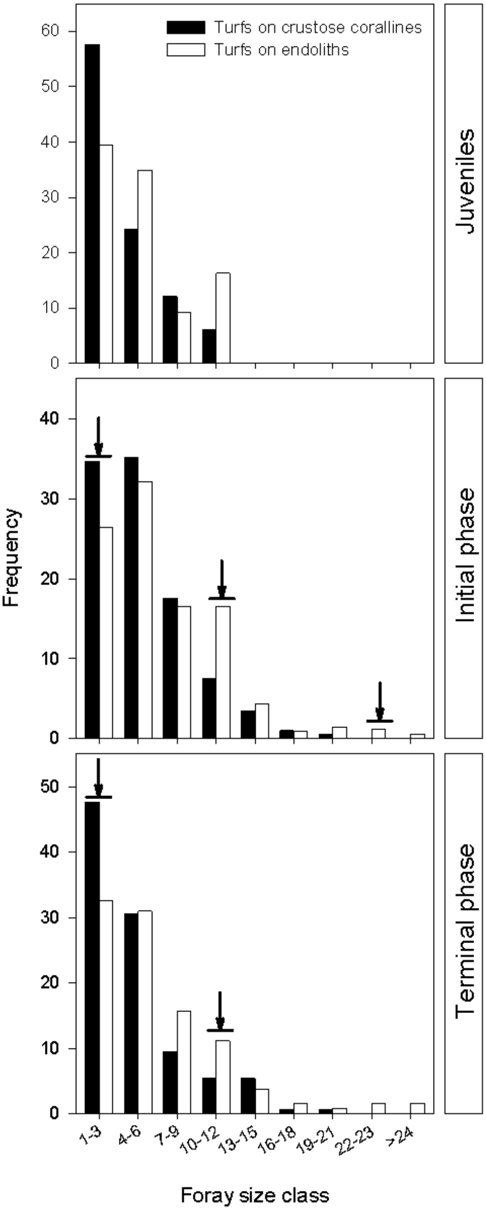

Fig. 3.7 *Scarus ferrugineus.* Frequency distribution of foray size classes for the two main biota. Arrows on bars show the foray classes that made significant contributions to the difference.

63.721, $P = 0.000$; hot season: 18.164, $P = 0.004$; Fig. 3.8). Step wise elimination indicated that choice of feeding surface in the morning differed significantly from the other two periods which were similar to each other. In summary, *S. ferrugineus* feeds more from coral bases and vertical surfaces in the morning than during other times of day. During the afternoon 60% of bites are taken from horizontal surfaces, as opposed to 40% in the morning.

3.3.7 Scraping capacity

Percentage of bites producing visible grazing scars increased significantly with fish size (ANCOVA: $F_{2,9} = 19.766$, $P = 0.003$; Fig. 3.9). For the largest size class, 70% of bites produced scars. Life phases did not differ in their capacity to produce scars (ANCOVA: $F_{2,9} = 0.05$, $P = 0.946$). The effect of dead coral genus on scar production was tested for the common coral genera; *Echinopora*, *Lobophyllia*, *Montipora*, *Platygyra*, *Porites*, and *Stylophora*. The dead coral genus affected the percentage of bites producing scars significantly (ANCOVA: $F_{2,81} = 3.050$, $P = 0.015$). Pair wise contrasts revealed that the overall difference was caused by *Montipora* substrates, showing higher incidence of bite scars than *Stylophora* and *Echinopora* (ANCOVA pair-wise contrasts: $p<0.05$ for both).

3.4 Discussion

3.4.1 Spatial and seasonal aspects of resource abundance

Each of the three reef zones studied offered a different suite of substrates and biota for grazing fish. The cover of living corals (20 – 48%) is among the highest reported for the southern Red Sea (Zekeria & Videler 2000). Folios and canopy forming macroalgae are restricted to the shallow parts of the reef crest and the reef flat, where their density and biomass is controlled by seasonal changes in environmental conditions (Ateweberhan et al. 2006a). The absence of macroalgae in the deeper parts of the reef throughout the year strongly suggests that grazing prevents the development of macroalgae in these zones (this study). The reef crest with its high cover of epilithc algae (Klumpp & Mckinnon 1992, this study) and high productivity (Klumpp & Mckinnon 1989) appears to be the primary zone of foraging for coral reef grazers as indicated by their high densities at this zone (Bouchon-Navaro & Harmelin-Vivien 1981; Russ 2003; Fox & Bellwood 2007).

The composition of the biota also varied for the different parts of dead coral substrate. The prevalence of crustose corallines on cryptic surfaces such as coral bases, overhangs and the understory of algal canopies is common and is attributed to factors such as low grazing, low sedimentation and shading from intense light (Baynes 1999; Caragnano et al. 2009). Conversely, the dominance of turf algae on exposed surfaces may be related to their ability to tolerate high light intensities, sedimentation and intense grazing (Carpenter 1985; Hackney et al. 1989).

Resource abundance varied significantly with season in the two shallower zones but remained unchanged in the deep fore reef. This may be due to the smaller seasonal variations in temperature and irradiance at 10 m depth compared to the shallower areas. Hatcher and

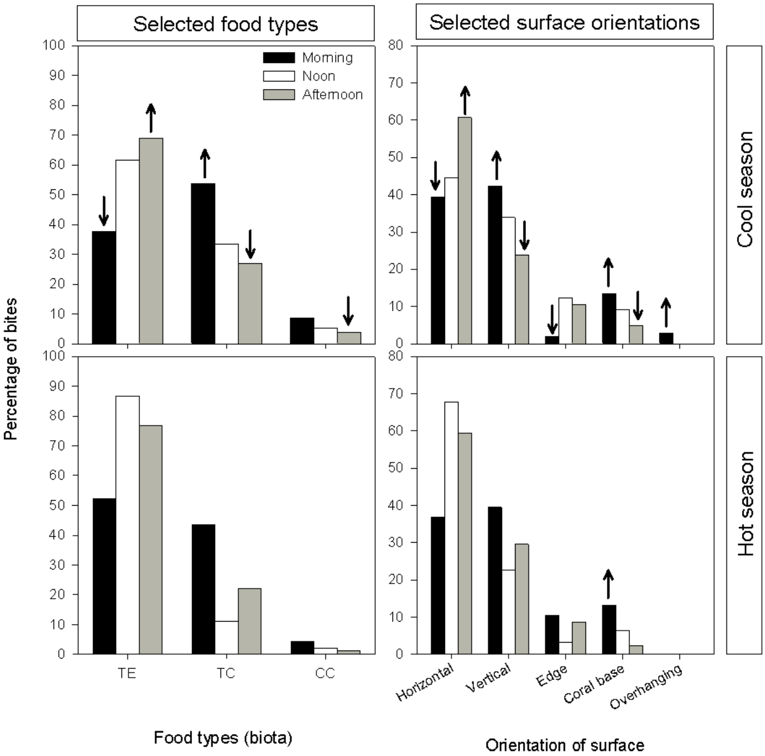

Fig. 3.8 *Scarus ferrugineus*. Diurnal change in the percentage use of biota and dead coral surfaces during the cool and hot seasons. Arrows indicate components that were used significantly less (downward pointing) or more than expected (upward pointing). See caption of Figure 5 for explanation of the acronyms.

Larkum (1983) described a similar trend of decreasing seasonality with depth in the Great Barrier Reef (GBR). In the reef crest and shallow fore reef zones, crustose corallines and macroalgae (only on the reef crest) attain higher cover and biomass (Ateweberhan et al. 2006a) during the cool season. At the onset of the hot season, rising temperatures and irradiance cause crustose corallines, foliose and canopy forming macroalgae to decline (Ateweberhan et al. 2005a; Ateweberhan et al. 2005b; Ateweberhan et al. 2006b) creating opportunity for the tolerant turfs to increase in cover (Ateweberhan et al. 2006a).

3.4.2 Utilisation of grazing substrates

S. ferrugineus feeds almost exclusively from dead coral substrates with a small percentage of bites taken from coral rubble and limestone pavement. *S. ferrugineus*, as many other parrotfishes (e.g., Bruggemann et al. 1994a; Bellwood 1995a), rarely bites on living corals. Preference for dead coral substrates is widely reported for many parrotfishes species in the Caribbean (Bruggemann et al. 1994a), GBR (Bellwood 1995a), and Red Sea (Alwany et al. 2009). One possible explanation for this is the prevalence of preferred algal food types among the biota that occupy dead coral surfaces (Bruggemann et al. 1994a). Similarly, the underutilization of coral rubble appears to be related to the dominance of crustose corallines, a non-preferred food item, on this substrate. Limestone pavements being flat are prone to high sediment loads, a condition known to deter grazing in some herbivorous fishes (Bellwood & Fulton 2008).

Not all dead coral substrates were equally targeted by *S. ferrugineus*. *Porites* is the most consistently preferred dead coral receiving the bulk of the bites, particularly in the reef crest and shallow fore reef zones. Comparable high selectivity is reported for the excavating parrotfish *Sparisoma viride* which prefers to feed on dead *Montastrea annularis* and *Madracis mirabilis* colonies (Bruggemann et al. 1994b). This was attributed to the relatively low skeletal density of these substrates and the resulting higher yield per bite. Other characteristics of these commonly targeted coral genera that may be selected for are their massive growth form and their relatively smooth surface (due to their small calyx sizes). Besides permitting relatively high yields, preference for these genera may be linked to the ease at which medium sized parrotfishes can take bites without damaging their dentition (Bonaldo et al. 2007). Parrotfish grazing efficiency may thus be limited by the surface characteristics of the substrate. Rugged and branching structures can function as grazing refuges for macroalgae (Bennett et al. 2010).

Juveniles differed from the adults in that they restricted their bites exclusively to dead coral colonies. This may be due to the increased predation risk on flat open spaces (Connell & Jones 1991) where limestone pavement and coral rubble predominate. Most bites of *S. ferrugineus* targeted convex surfaces. This contrasts with reports showing that excavators use convex surfaces more than scraping species do (Bellwood & Choat 1990; Bruggemann et al. 1994a). A possible explanation for this may be a lack of competition for this niche from excavating species, such as *Chlorurus sordidus*, whose abundance in the present study site is an order of magnitude less than that of *S. ferrugineus*.

3.4.3 Choice of biota

Similarity in resource use among the different life phases of *S. ferrugineus* is in agreement with similar reports on other parrotfishes (Bruggemann et al. 1994a; Bonaldo et al. 2006). However, post-settlement scarids are omnivorous including a large proportion of crustaceans and foraminifera in their diet (Bellwood 1988). The transition to a diet composed of epilithic algal community is estimated to occur between sizes of 1.5 to 3 cm (Chen 2002). The juvenile size classes included in this study (4 – 8 cm) are therefore likely to represent individuals that are past this omnivorous phase.

S. ferrugineus is a selective feeder predominantly foraging on turfs on endoliths and turfs on crustose corallines. These represent >90% of the bites during both seasons and in all reef zones. Crustose corallines, macroalgae and living corals are consistently underutilized compared to their availability. Preference for turfs on endoliths has been reported for two other parrotfishes from the Caribbean (Bruggemann et al. 1994b,a). Most other studies on parrotfish feeding preference have not made the distinction between turfs growing on endoliths and those growing on crustose corallines (e.g., Hatcher & Larkum 1983; Bellwood 1995a). It

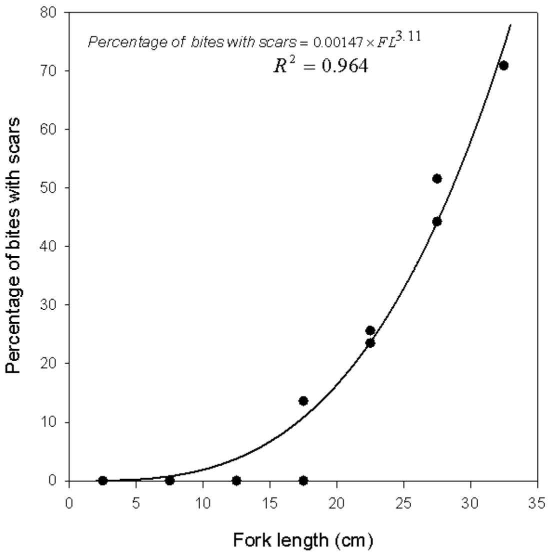

Fig. 3.9 *Scarus ferrugineus*. Percentage of bites that produce visible scars as a function of fish fork length (FL).

is therefore difficult to compare their results with our findings. Bruggemann et al. (1994b) analyzed the nutritional quality and biomass of the different epilithic algal communities in the Caribbean and concluded that turfs on endoliths have higher nutritional quality as well as biomass compared to turfs on crustose corallines. Moreover the higher biomass of turfs on endoliths is likely to contain higher concentration of the detritus (Purcell & Bellwood 2001; Wilson et al. 2003), which has been shown to be nutritionally richer than epilithic algae alone (Wilson et al. 2003).

The endolithic component of turfs on endliths can make up 32 – 46% of the net community production on carbonate substrates (Tribollet et al. 2006). This constitutes a significant potential source of energy for those species that are capable of denuding the substrate – namely large-bodied scrapers and excavating species. While all life phases of *S. ferrugineus* target the same biota, the actual intake may differ among life phases due to size related differences in their scraping capacities (Fig. 3.9) (Bonaldo & Bellwood 2008; Lokrantz et al. 2008). Large TP fish - owing to their higher scraping capacity - can be expected to utilize this endolithic component to a greater extent.

3.4.4 Diurnal changes in food selection

The shift in feeding preference of *S. ferrugineus* in different daytime periods recorded in the present study is associated with changes in the exploitation of grazing surfaces with different orientation. Surfaces of different orientation are associated with different algal types, resulting in the observed diurnal shift in feeding selection. This feeding pattern appears to coincide with the predictions of the diel feeding hypothesis, which states that herbivorous fish optimize their food intake by targeting highly productive algae in the afternoon to harvest readily digestible photosynthetic products (Polunin & Klumpp 1989; Zemke-White et al. 2002). Indeed, production and nutritional quality in turf algal communities increases through the morning reaching its peak at noon (Bruggemann et al. 1994; Zemke-White et al. 2002). In the southern Red Sea, *S. ferrugineus* seems to respond to the low nutritional quality of turfs in the morning both by lower feeding rates (Y.A., pers. obs.) and by including other, less preferred food sources. A combination of these two responses leaves turfs on endoliths relatively untouched until late morning. Related to this, grazers are known to respond to spatial differences in turf algal production by aggregating on areas with high production (Klumpp & Polunin 1990; Russ & McCook 1999; Russ 2003; Burkepile & Hay 2009). Together, these findings suggest a close link between algal turf community production and the spatial and temporal patterns of feeding in grazing fishes.

Recent studies on the nutritional ecology of scarids have indicated detritus as a dominant food source for this group (Choat et al. 2002; Crossman et al. 2005). At our study site, late night and morning periods are characterized by calm conditions that promote deposition of particulate organic material (Crossman et al. 2001; Purcell & Bellwood 2001). If such detrital matter constitutes a primary food source, scarids can be expected to adapt their feeding pattern to optimize its intake by high feeding rates on horizontally exposed surfaces in the morning. This clearly contradicts our findings. However, the actual definition of 'detritus' also incorporates fresh photosynthetic products exuded by algal turfs, endolithic algae and associated microflora. Recent studies have shown that the bulk of the organic matter in detritus is derived from the epilithic algae (Wilson et al. 2001; Wilson et al. 2003) a significant portion which consists of freshly exuded photosynthetic products (Wilson et al. 2001). Quantity and quality of detritus will therefore be expected to have a similar diurnal rhythm as epilithic algae (Wilson 2002). Scarids targeting such organic matter would be expected to exhibit feeding patters similar to those observed in this study. Further studies are required to distinguish deposited detrital material from locally produced photosynthetic exudates and their utilisation by grazing parrotfishes.

3.4.5 Seasonal aspects of food choice

Resource use in *S. ferrugineus* varied between the cool and the hot seasons, but only in the shallower reef zones where significant seasonal changes in abundance of algal functional groups occurred. Reduced availability of turfs on endoliths - the preferred food type - in the cool season resulted in increased utilization of the second important food type turfs on crustose corallines. This increased exploitation of turfs on crustose corallines however did not extend to crustose corallines and macroalgae, algal functional groups that become abundant during the cool season. Moreover, reduced availability of the primary food type did not result in an increase in the niche breadth. It appears that *S. ferrugineus* shows limited flexibility in resource use, feeding mainly on turfs associated with hard coral substrates. Given the low availability of their main food source and the lower feeding rates during the cool season, *S. ferrugineus* may well be energetically limited during this period of the year. This notion is supported by observations of low liver fat reserves and growth rates during the cool season (Chapters 5, 7).

Our results suggest that *S. ferrugineus* shows limited flexibility in its feeding behaviour in the face of large seasonal changes in the composition and production of different functional groups of algae. In particular the large seasonal build-ups of macroalgal biomass on the reef crest and reef flat remain largely unexploited. This is consistent with other studies (McClanahan et al. 1999; Bellwood et al. 2006; Ledlie et al. 2007; Mantyka & Bellwood 2007; Fox & Bellwood 2008b) that have reported limited impact of scarids on well established mature macroalgal stands.

Acknowledgments: We gratefully acknowledge assistance of Negassi Ghirmay, Yosief Hiabu, Woldeselassie Hidray and Siraj Mohammed and the support of the Netherlands Foundation for the Advancement of Tropical Research (WOTRO grant W84-589). We thank three reviewers for valuable comments on the manuscript.

A3 Appendix

A3.1 Sampling of benthic communities

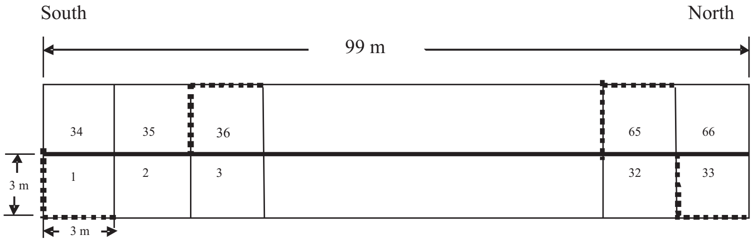

Fig. A3.1 Diagram showing the placement of chain-links in randomly selected 3 m x 3 m quadrats. In this example, quadrat numbers 1, 33, 36 and 65 were randomly selected. Broken lines indicate sides of the quadrat where the chain–links were laid.

A3.2 Relationship between surface orientation of a dead coral and the epilithic community

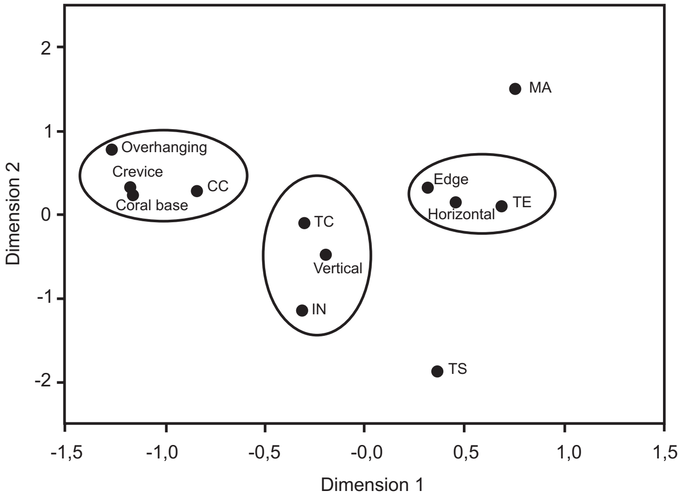

Fig. A3.2 Association of different benthic categories with the surface orientation of dead coral colonies. Figure by John Videler.

A3.3 Substrate composition of the Sheikh Said Island fringing reef

Table A3.1 Relative abundance of substrates on three reef zones of Sheikh Said Island for the cool season, hot season and for both seasons (pooled). Relative abundance is expressed as the percentage of total chain-links.

Reef zone	Season	Living coral	Dead coral	Coral rubble	Limestone pavement	Sand	#chain-link points
Reef crest	Cool	23.5	24.0	17.8	21.6	13.1	5347
	Hot	22.9	28.5	16.6	20.9	11.2	4266
	Pooled	23.2	26.0	17.2	21.3	12.3	9613
Shallow fore reef	Cool	18.7	28.9	21.1	1.6	29.7	5415
	Hot	22.3	27.7	21.0	0.9	28.1	5497
	Pooled	20.5	28.3	21.1	1.2	28.9	10912
Deep fore reef	Cool	46.7	21.8	7.1	4.8	19.6	5066
	Hot	50.1	25.2	5.5	1.8	17.30	3799
	Pooled	48.2	23.3	6.4	3.5	18.60	8865

A3.4 Feeding preference of the different life phases of *S. ferrugineus*.

Table A3.2 *Scarus ferrugineus*. Summary of available food items and their utilization by Initial Phase (IP), Terminal Phase (TP) and Juvenile (JU) fish. Availability and utilization are given as the percentage of total chain-links or total bites respectively. Values in brackets: number of bites described. Last column shows chi-square tests of: Upper values: selectivity pooled over all life phases. Lower values: Comparison of utilization among life phases. Bold values are statistically significant.

Zone	Season	Life phase	Turfs on endolithic algae	Turfs on crustose corallines	Crustose corallines	Macroalgae	Turfs on sponges	Invertebrates	Pearson Chi-square χ^2 (df); P
Reef crest	Cool*	Available	24.4	28.0	37.4	9.8	0.0	0.3	Available vs. Used: $\chi^2(3) = 108.25$; $P =$ **0.000** IP vs. TP: $\chi^2(2) = 3.26$; $P = 0.196$
		IP (92)	46.7	51.1	2.2	0.0	0.0	0.0	
		TP (77)	44.2	44.2	6.5	5.2	0.0	0.0	
	Hot	Available	45.1	33.2	21.2	0.1	0.0	0.4	Available vs. Used: $\chi^2(3) = 64.28$; $P =$ **0.000** IP vs. TP vs. JU: $\chi^2(4) = 1.95$; $P = 0.744$
		JU (62)	59.0	39.3	1.6	0.0	0.0	0.0	
		IP (113)	65.5	31.9	2.6	0.0	0.0	0.0	
		TP (85)	69.1	28.6	2.4	0.0	0.0	0.0	
Shallow fore reef	Cool*	Available	33.1	27.7	37.9	0.0	0.0	1.3	Available vs. Used: $\chi^2(3) = 176.58$; $P =$ **0.000** IP vs. TP: $\chi^2(2) = 0.33$; $P = 0.847$
		IP (275)	55.4	38.0	5.5	0.0	0.4	0.7	
		TP (154)	52.6	40.8	5.9	0.7	0.0	0.0	
	Hot	Available	37.1	39.3	21.6	0.0	0.1	1.9	Available vs. Used: $\chi^2(3) = 256.59$; $P =$ **0.000** IP vs. TP vs. JU: $\chi^2(4) = 5.94$; $P = 0.203$
		JU (43)	67.5	30.0	2.5	0.0	0.0	0.0	
		IP (351)	69.5	28.9	1.4	0.3	0.0	0.0	
		TP (209)	72.1	25.5	2.4	0.0	0.0	0.0	
Deep fore reef	Cool*	Available	42.6	33.2	12.3	0.0	2.1	9.9	Available vs. Used: $\chi^2(3) = 16.80$; $P =$ **0.001** IP vs. TP $\chi^2(2) = 1.27$; $P = 0.531$
		IP (18)	77.9	16.7	0.0	0.0	5.6	0.0	
		TP (29)	66.7	29.6	3.7	0.0	0.0	0.0	
	Hot	Available	30.1	51.1	11.1	0.0	1.5	6.2	Available vs. Used: $\chi^2 3 = 31.67$; $P =$ **0.000** IP vs. TP vs. JU: $\chi^2 4 = 3.08$; $P = 0.545$
		JU (23)	52.2	43.5	0.0	0.0	4.4	0.0	
		IP (34)	52.9	29.4	0.0	0.0	17.7	0.0	
		TP (41)	53.7	36.6	0.0	0.0	9.8	0.0	

* During the cool season only bites from IP and TP were described since JU were rare.

CHAPTER 4

FOOD INTAKE BY THE PARROTFISH *SCARUS FERRUGINEUS* VARIES SEASONALLY AND IS DETERMINED BY TEMPERATURE, SIZE AND TERRITORIALITY

Y. Afeworki, Z.A. Zekeria, J.J. Videler, & J.H. Bruggemann

Abstract On coral reefs feeding by parrotfishes may prevent coral to macroalgal phase shifts by keeping algae in a cropped state. To predict the response of grazers to changing conditions, knowledge of the factors that affect feeding intensity is needed. Therefore we studied food intake of the parrotfish *Scarus ferrugineus* on an inshore fringing reef in the southern Red Sea, Eritrea, where seasonality and extreme summer temperatures were expected to influence feeding rates. Bite rates (bites min^{-1}), defecations min^{-1} and yield per bite (mass ingested $bite^{-1}$) were estimated for three categories: 20 – 25 cm initial phase (IP), 30 – 35 cm terminal phase (TP) and 30 – 35 cm territorial TP (TTP). The bite rates increased from low levels in the morning to peak values in the afternoon. Bite rate of IP increased linearly with sea water temperature. For TP, the temperature-bite rate relationship was quadratic, with maximum bite rates at 32°C and lower rates at higher temperatures. Yield per bite in both IP and TP did not differ with time of year. Throughout the year, the total daily bites were highest in IP and lowest in TTP. Territorial activity costs 23% lower daily intake in TTP compared to similar-sized TP males. Daily intake of ash-free dry mass of epilithic algal matrix (g AFDM d^{-1}) was 7.5 – 9.6 for IP, 12.4 – 17.5 for TP and 8.7 – 13.2 for TTP. Intake and defecation rates and hence gut turnover rates peaked from April to July. The quadratic temperature response of TP suggests that large individuals may be close to their upper thermal limit, implying that temperature rises are likely to negatively affect grazing by large-bodied parrotfishes.

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4.1 Introduction

Marine herbivorous fishes achieve the highest densities and diversity in tropical coral reef ecosystems (Meekan & Choat 1997; Floeter et al. 2005). Grazing rates on coral reefs are known to be extremely high, being capable of removing 50 – 90% of the daily production of turf algae (Hatcher 1982; Klumpp & Polunin 1990; van Rooij et al. 1998; Paddack et al. 2006). The primary grazing target is the epilithic algal matrix (EAM), composed of algal turfs with associated biota and detritus (Wilson et al. 2003). Despite its low standing crop, the EAM is known to support high grazer biomass due to high productivity (Carpenter 1985; Klumpp & Mckinnon 1989).

Parrotfishes often represent a large proportion of the total grazer biomass (van Rooij et al. 1998; Williams & Polunin 2001). Most parrotfishes feed by scraping or excavating the EAM from dead coral matrix (Bellwood & Choat 1990; Bruggemann et al. 1994a). This feeding action is a major structuring force of coral reef benthic communities, controlling the biomass and distribution of benthic algae, enhancing coral recruitment and generally promoting reef recovery (Mumby et al. 2007; Mumby & Harborne 2010). Despite their low quality diet parrotfishes show fast growth rates (Russ & St.John 1988; van Rooij et al. 1995b). Compared to the other similar sized fishes such as acanthurids, parrotfishes generally have shorter life span (Choat et al. 1996; Choat & Robertson 2002) and suffer higher predation rates (Sudekum et al. 1991; Kingsford 1992). These traits suggest high turnover in parrotfish populations and a throphodynamically important role for these grazers in coral reef ecosystems.

Behavioural aspects of parrotfish foraging such as patterns in habitat use, preference for substrates and bite rates have been studied extensively (Bouchon-Navaro & Harmelin-Vivien 1981; Bruggemann et al. 1994b; Afeworki et al. 2011; Afeworki et al. 2013). Bite rates in parrotfish vary as a function of innate factors such as body size, social status and feeding mode (excavator vs scraper) (Bruggemann et al. 1994; Bruggemann et al. 1994a; Bonaldo et al. 2006) and environmental factors such as temperature, nutritional quality, and productivity (Carpenter 1988; Targett & Targett 1990; Ferreira et al. 1998; Russ & McCook 1999; Smith 2008).

Temperature is perhaps the most critical determinant of intake rate in ectotherms. The hump-shaped relationship between temperature and food intake indicates limits to intake rate at both low and high temperatures (Horn & Gibson 1990; Koskela et al. 1997; Saoud et al. 2008; Englund et al. 2011). The emphasis of past research on coral reefs has been on limits to grazing at low temperatures (Horn 1989; Floeter et al. 2005; Smith 2008). It is not known whether rising temperatures will promote or suppress grazing in coral reefs. Individual grazing rates could increase due to rises in temperature (Smith 2008). Conversely higher temperatures may lead to communities dominated by smaller bodied individuals (Munday et al. 2008; Barneche et al. 2009; Daufresne et al. 2009), which may reduce grazer impact and coral reef resilience.

Coral reefs in extreme environments such as the Arabian Gulf and southern Red Sea provide useful settings to explore how rising temperatures may impact coral reefs in future (Ateweberhan 2004; Feary et al. 2010). Inshore reefs of the southern Red Sea are characterized by extreme summer temperatures (>33°C at 2 m depth) that are higher than in most coral reef areas (Ateweberhan et al. 2005b). Moreover, regional sea surface temperatures have shown a rapid increase of 0.7°C since the mid-1990s (Raitsos et al. 2011). Temperatures as high as 36°C on shallow reef flats have been implicated as a cause for lower grazing rates in this zone during summer (Ateweberhan et al. 2006a; Afeworki et al. 2013). Despite a relatively narrow annual temperature range (<10°C), the area experiences significant seasonal changes in productivity and community composition of benthic algae (Ateweberhan et al. 2006a), fish growth (Zekeria et al. 2006), and recurrent bleaching of corals (YA & JHB personal observations). This is mainly because the summer temperatures are extremely high, causing many of the benthic communities to persist close to their upper critical temperatures (Ateweberhan et al. 2005b; Ateweberhan et al. 2006a). In this study, we make use of this seasonality to investigate the effects of extreme summer temperatures on bite rates and food intake by different social categories of *Scarus ferrugineus* on an inshore fringing reef in the southern Red Sea.

4.2 Materials and methods

4.2.1 Study site and species

The study was conducted on the shallow fringing reefs of Sheikh Said Island (15°35′N; 39°29′E) in the southern Red Sea, Eritrea between 2005 and 2007. For a detailed description of the study site see Ateweberhan et al. (2006a) and Afeworki et al. (2011). Mean monthly sea surface temperature (SST) at 2 m depth ranges from 27.7°C in January to 33.4°C in August (Ateweberhan et al. 2006a). This monsoon-driven seasonality in SST is associated with significant changes in the composition, cover and biomass of benthic algae (Ateweberhan et al. 2006a). Turf algae, the primary food source of *S. ferrugineus*, achieve their highest cover during the hot season (Ateweberhan et al. 2006a; Afeworki et al. 2011), while foliose and canopy forming macroalgae dominate the shallow reef zones during the cool season (Ateweberhan et al. 2006a).

S. ferrugineus is the dominant grazer on the reefs of the southern Red Sea constituting about 34% of the total biomass of herbivorous fishes (Afeworki et al. 2013). This species forages primarily on the reef crest and shallow fore reef zones (Afeworki et al. 2011). Like most other labrids, *S. ferrugineus* is a protogynous hermaphrodite with two distinct life phases: the drab Initial female Phase (IP), and the colourful Terminal male Phase (TP) (Randall & Ormond 1978). A subset of the TPs keep temporary spawning territories outside the main foraging zones and are considered as a third category "Territorial TP" (TTP). IP reach 26 cm in length, TP 36 cm. Three size and social categories are the main focus of this study: 20 – 25 cm IP (henceforth IP), 30 – 35 cm TP (henceforth TP) and 30 – 35 cm territorial TP (henceforth TTP).

4.2.2 Bite and defecation rates

Haphazardly selected individuals of *S. ferrugineus* were allowed to acclimatize to the presence of the observer for three minutes. The fork length, life phase, time of day and date were recorded. Selected individuals were observed for 5 – 15 minutes and the number of bites and defecations recorded, either directly in the field or from underwater videos recorded by following a focal fish with a handheld camera (Sony digital camera Model no: DSC-W17). Bite and defecation rates were calculated as number of bites (defecations) min^{-1}. All observations were made by snorkelling or SCUBA. Due to the absence of spear fishing or fish feeding by divers, observations at close range (<0.5 m distance) are possible with no discernible change in behaviour of focal fish. Underwater size estimation was practiced with PVC pipes of known length or by estimating fish size before spearing them. Furthermore, size of videoed individuals was estimated from frames with objects of known dimensions as a scale.

Bite rates were sampled in 2-month periods (henceforth period), by combining months with similar SST (see Supplementary material for details). Periods are nested within the two distinctive southern Red Sea seasons, the cool (December – March) and the hot season (May – October) (Ateweberhan et al. 2006a). Dawn-to-dusk observations of feeding were made on focal IP and TP fish while feeding observations of TTP were conducted during spawning episodes. To determine the beginning and the end of the feeding day, several dives were conducted around sunrise and sunset to record the first and last bites for most periods except April – May, where the values of August – September, a period with similar day lengths, were taken. Complete dawn-to-dusk records of defecations were made during the February – March and October – November periods only. During the other periods (except April – May), defecation rates were recorded between 1100 – 1800 hrs.

4.2.3 Bite rates, total daily bites and daily intake rates

Bite rate was plotted against time (minutes after midnight) and a polynomial quadratic function fitted to the data from IP, TP and TTP fish. A second order polynomial was selected because it fitted data best; it has been successfully used to explain feeding patterns in scarids (Bellwood 1995b; Ong & Holland 2010). The cumulative number of bites taken per day (TDB) is the area under this curve delimited by the beginning and the end of the feeding day. TDB was determined for each month and life phase category. Daily intake rate was estimated as the product of TDB and yield per bite.

4.2.4 Yield per bite

The amount of food ingested per bite was estimated using a modification of the gut-fullness method (Montgomery 1980; Polunin 1988). IP and TP fish were speared throughout the morning hours between the start of feeding and first defecation in February and in October. Plots of defecation rates against time of day were used to identify the time when defecation commences (Fig. 4.5). Mass of empty guts was determined from a different group of fish that were captured using a barrier net and kept overnight *in situ* in perforated barrels to allow them to evacuate their gut contents. Collected fish were kept chilled and transported to the lab for dissection. The entire gut, from the oesophagus posterior of the pharyngeal mill to the anus was excised. Dry mass (DM) (after drying at 60°C for 24 hours) and ash free dry mass (AFDM, after burning in a muffle furnace at 550°C for 8 hours) of the gut plus contents was determined to the nearest 0.01 g. The cumulative number of bites a fish had taken prior to being speared was estimated from the area under the bite rate curves (Fig. 4.4) delimited by the start of feeding until the time the fish was speared. The slope of the regression line of gut mass (DM or AFDM) against number of bites gives the yield per bite in g DM or g AFDM bite^{-1}.

4.2.5 Statistical analysis

Bite rates of *S. ferrugineus* determined from direct field observations and videos were not different for any of the periods (ANOVA: $F_{1,283} = 1.16$, $P = 0.28$), hence these data were pooled for further analysis. ANCOVA was used to test differences in bite rate among life phases, taking life phase as a fixed factor and fork length as a covariate. Comparison of bite rates between TP and TTP was conducted by ANOVA. Relationships between monthly mean SST and monthly mean bite rate were established using regression models in SPSS and the best fitting curve was selected based on R^2 values.

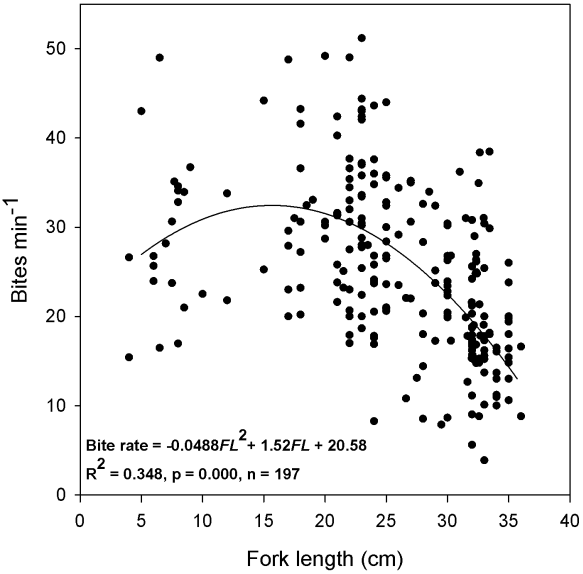

Fig. 4.1 Relationship between fork length (*FL*) and bite rate for *Scarus ferrugineus* in the southern Red Sea during June – July and August – September.

Every day between 0600 hrs and 1300 hrs TTP are engaged in either of two activities (states): foraging in the shallow reef zones or defending a spawning territory at the deep fore reef. Spawning activity lasted approximately 3 hrs, i.e. about 50% of the morning, with the exact timing depending on tidal state (Chapter 7). In this case, a reasonable approach to estimate the mean bite rate for the morning hours is to give equal chance for observations taken during spawning and none-spawning periods. Therefore, TTP bite rates before 1300 hrs were analysed by randomly taking equal numbers of observations from both states. For the period period 1300 hrs and beyond all bite rate data of TTPs were recorded during none spawning periods. To compare differences in yield per bite between the two periods, ANCOVA was conducted by taking gut DM as a dependent variable, cumulative number of bites as a covariate and period and life phase as factors. When no difference was detected between periods, linear regression was conducted on the pooled data to estimate the slope i.e. the yield per bite.

Linear combinations of dependent parameters were used to estimate variances and confidence intervals of TDB. Differences in TDB between months and the three life phase categories were compared using the Z-test in combination with the false discovery rate procedure to correct for multiplicity (Benjamini & Hochberg 1995). The overall error term for the daily intake rate was estimated by adding the relative uncertainties in TDB and yield per bite (propagation of error). Prior to conducting parametric tests, assumptions of normality and equality of variances were verified respectively using Kolmogorov-Smirnov and Levene tests in the Explore procedure of SPSS for Windows 16 (2007).

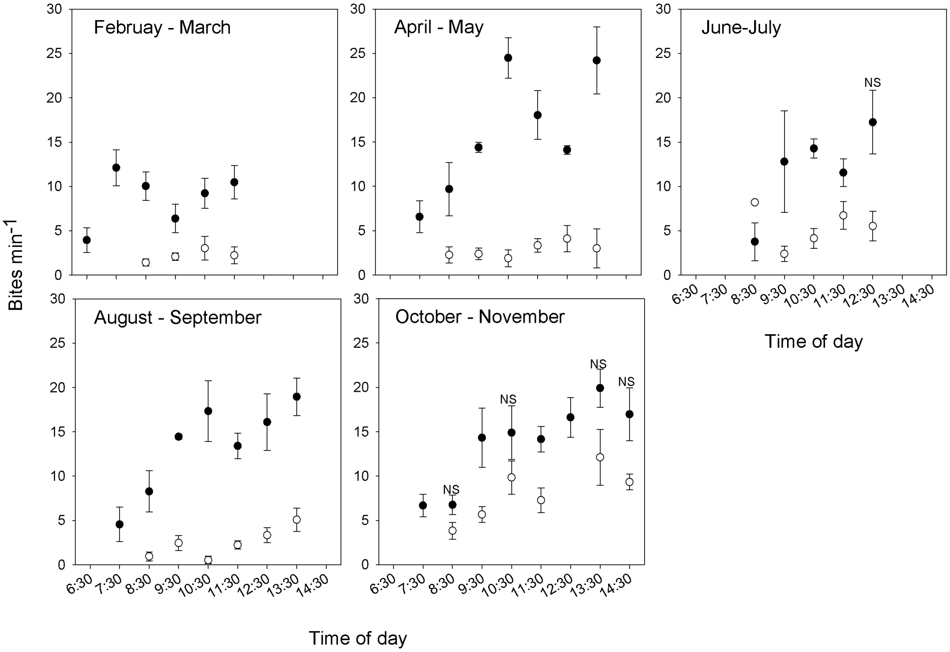

Fig. 4.2 Bite rates (means±SE) of large (30 – 35 cm) territorial terminal phase males (TTP) and none territorial terminal phase (TP) of *Scarus ferrugineus* for periods when TTP are keeping a temporary spawning territory in the deep fore reef and none territorial TP (TP) are foraging at shallow reef zones. NS: No significant difference in bite rate between TTP and TP within a time period.

4.3 Results

4.3.1 Bite rates

Bite rate was significantly different between the two size classes and among periods (ANCOVA: size: $F_{1,379}$ = 210.151; P = 0.000; period: $F_{4,379}$ = 7.63; P = 0.000). There was no interaction between period and fish size suggesting that size differences in bite rate are similar throughout the year. Bite rate was higher in the smaller size class (IP) than in the larger one (TP). Tests conducted on a separate data set (see Supplementary material) indicate that similar sized IP and TP fish have equal bite rates, suggesting that the observed difference is the effect of body size and not of life phase. Analysis of a larger dataset, including fish sizes outside the focal groups discussed here (see Supplementary material), demonstrated that fish size and bite rate are related by a quadratic function (Fig. 4.1) with peak values around 15 – 20 cm.

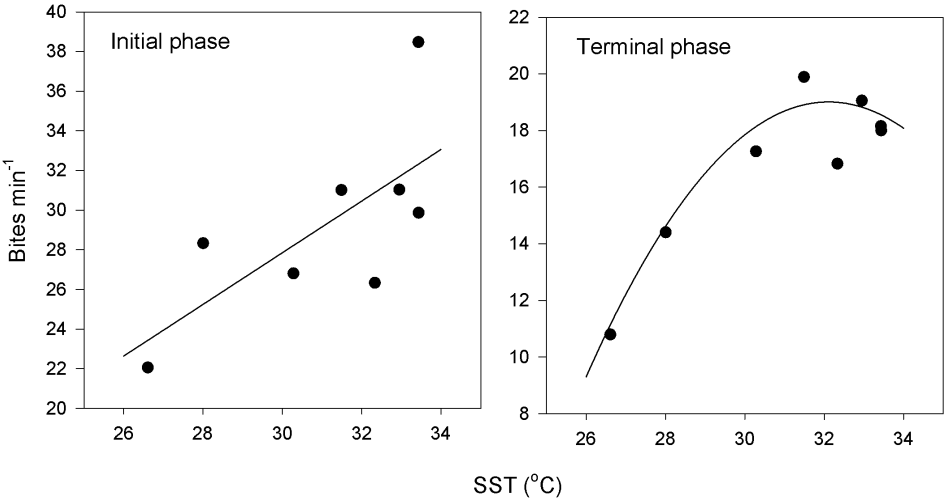

Fig. 4.3 Relationships between monthly mean SST and mean bite rate of *Scarus ferrugineus* during the peak feeding time (1200 – 1800) for IP (20 – 25 cm forklength) and TP (30 – 35 cm forklength) fish. Note the difference in scale of Y-axis.

During spawning episodes the bite rate of TTP was significantly lower than those of similar sized TP (Fig. 4.2). Bite rates were highest during April – May and lowest during February – March. Monthly mean SST has a significant effect on the bite rate of *S. ferrugineus*. For IP fish, bite rate increased linearly with SST ($R^2 = 0.496$, $F_{2,5} = 5.907$, $P = 0.051$, n = 8, Fig. 4.3), while for TP fish the bite rate declined when mean SST exceeded 32°C, such that a second order polynomial best described the relationship between SST and bite rate for this life phase ($R^2 = 0.905$, $F_{2,5} = 23.863$, $P = 0.003$, n = 8, Fig. 4.3).

For all life phases, bite rate increased steadily during the morning and reached peak values between 3 – 4 pm. This daily trend was strongest during the warmer months (Fig. 4.4). During the cooler February – March period this daily rhythm is weak and bite rates remain low throughout the day. This pattern is most pronounced in the larger size class.

4.3.2 Yield per bite

Gut DM increased linearly with the cumulative number of bites in both IP and TP (Fig. 4.6). Yield per bite did not differ between the two periods (interaction term in Table 4.1) for both life phases. Within each life phase the effect of fork length was not significant (ANCOVA: IP:

Table 4.1 *Scarus ferrugineus*: Summary of GLM results of gut dry mass (DM, g) and cumulative number of bites at two different periods of the year (February – March, October – November); MS: mean squares; df: degrees of freedom; F: ANOVA F-statistic; P: probability; significant effects in bold type.

Source	20 – 25 cm IP				30 – 35 cm TP			
	SS	df	F	P	SS	df	F	P
Bites	191.580	1, 38	162.633	**0.000**	414.984	1, 16	32.174	**0.000**
Period	2.010	1	1.706	0.200	5.212	1	0.404	0.537
Period*bites	0.044	1	0.037	0.848	32.754	1	2.539	0.137

$F_{1,16} = 2.532$, $P = 0.131$; TP: $F_{1,10} = 0.889$, $P = 0.368$). The overall value of the yield per bite for each size class was therefore estimated by pooling data from both periods (February – March and October – November) (see Table 4.2 & Fig. 4.6).

Table 4.2 *Scarus ferrugineus*: Parameter estimates of the linear regression of gut mass with the cumulative number of bites ($DM[orAFDM] = a \times Bites + b$). Also given are the coefficient of determination R^2, probability (P) and sample size (n).

	20 – 25 cm IP		30 – 35 cm TP	
	DM	AFDM	DM	AFDM
a	0.0049 (0.00037)	0.00054 (0.00019)	0.013 (0.0015)	0.0015 (0.00069)
b	2.16 (0.21)	1.75 (0.18)	3.71(1.66)	3.07 (0.88)
R^2	0.82	0.30	0.77	0.27
P	0.00	0.01	0.000	0.057
n	39	21	19	14

4.3.3 Total daily bites and daily intake rates

Estimates of TDB for both size classes are shown in Fig. 4.4. During all periods, TDB of IP was significantly higher than that of TP (Z-test: $P < 0.0005$), while TTP had a significantly lower TDB than TP in all periods (Z-test: $P < 0.0128$) except during October – November (Z-test: $P > 0.127$). In IP, TDB tended to be higher in the warmer months with the lowest number of bites recorded in February – March and October – November periods. For both TP and TTP fish, TDB peaked during the April – May period. Estimated daily intake (DM and AFDM) by IP, TP and TTP during different times of year is presented in Table 4.3.

4.3.4 Defecation rate

The daily pattern in defecation rate was investigated during the February – March and October – November periods. In both IP and TP defecation commenced abruptly between 9 – 10 am during the cold period (Fig. 4.5). However during the October – November period defecation in the IP started earlier, between 8 – 9 am. Once initiated, defecation remained

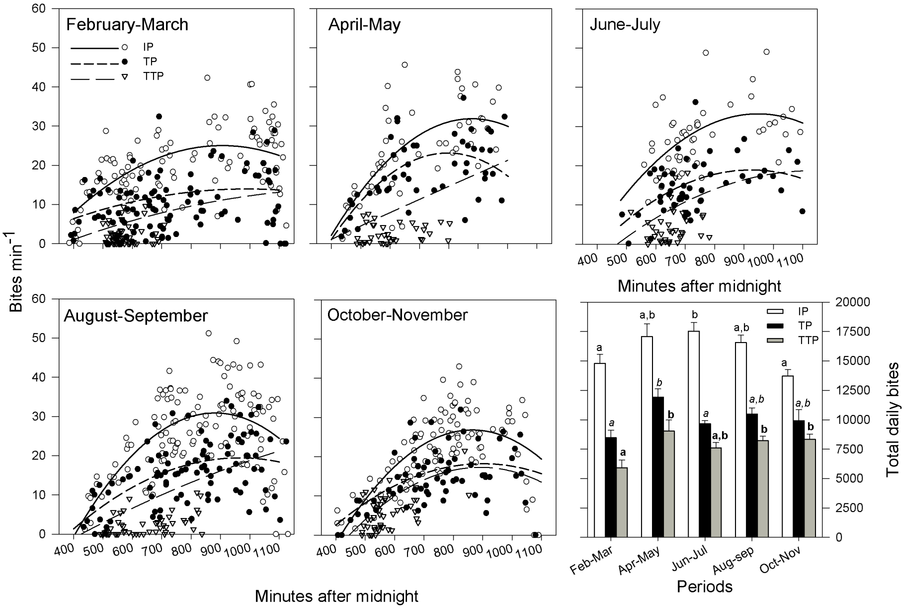

Fig. 4.4 Diurnal pattern in bite rates of initial phase (IP), terminal phase (TP) and territorial terminal phase males (TTP) of *Scarus ferrugineus* at different periods of the year. Lower right-hand panel: mean total daily bites (±SE) taken by IP, TP and TTP. For each life phase, significant differences between periods are indicated with different letters.

high throughout the day at a rate of 0.12 – 0.29 defecations min^{-1} for the IP and 0.09 – 0.18 for the TP (Fig. 4.5). The mean defecation rate showed a seasonal pattern similar to the bite rate. The defecation rate was generally higher during the warmer periods of the year when bite rates were also higher (Fig. 4.5). For the 20 – 25 cm size class, the difference in defecation rates between periods is significant (ANOVA: $F_{3,212} = 9.738$, $P = 0.000$), but the difference for the 30 – 35 cm size class is not (ANOVA: $F_{3,137} = 2.097$, $P = 0.103$).

4.4 Discussion

4.4.1 Bite rates, total daily bites and intake rates

Daily rhythm in bite rate in *S. ferrugineus* fits well with patterns reported for other herbivorous reef fishes including blennies, damselfishes, surgeonfishes and parrotfishes (Zemke-White et al. 2002). In all these groups bite rate tends to rise through the morning reaching peak values in the afternoon. This widespread phenomenon is believed to be driven by higher productivity and nutritional quality of turf algae later during the day (Polunin & Klumpp 1989; Zoufal & Taborsky 1991). In *S. ferrugineus* the weakest daily pattern was observed during the cool season

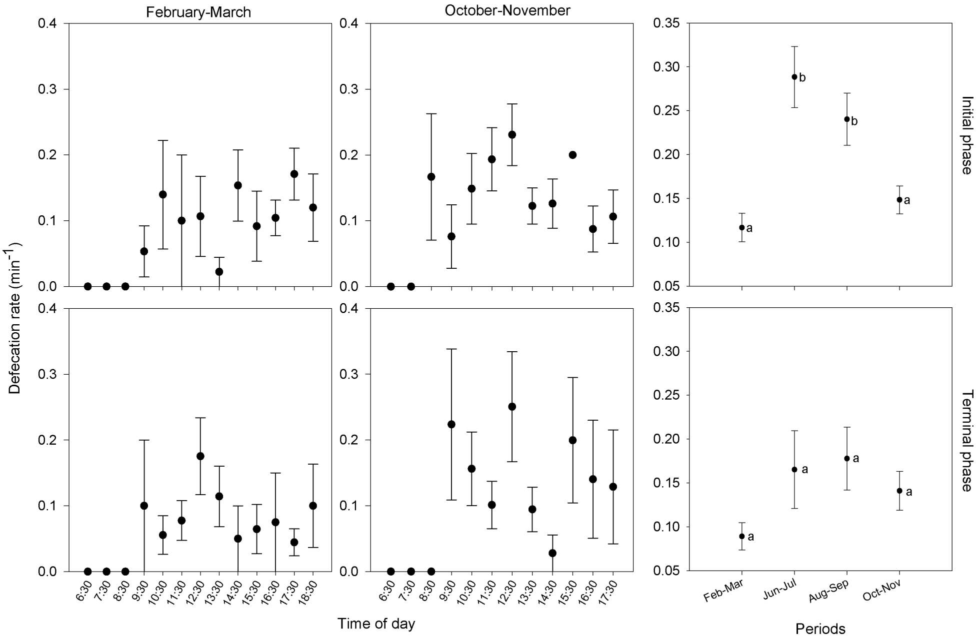

Fig. 4.5 Daily pattern of mean defecation rates (±SE) in initial phase (IP) and terminal phase (TP) of *Scarus ferrugineus* during February – March and October – November periods. Right-hand panels: mean defecation rates (±SE) in different periods. Significant differences between periods indicated with different letters.

(February-March); a season with the lowest primary production in turf algae (Ateweberhan et al. 2006a). The difference in productivity between morning and afternoon is expected to be more pronounced during the seasons of high solar radiation and high primary productivity (Polunin & Klumpp 1989; Ateweberhan et al. 2005a; Miller et al. 2011), leading to the observed stronger daily pattern of higher afternoon bite rates in the warm compared to the cool season.

Compared to other similar-sized scarids (Bellwood 1995b; Ong & Holland 2010), *S. ferrugineus* generally feeds at a higher rate and takes more bites per day, particularly during spring and summer. Defecation rates are the highest during this period indicating that the gut turnover rates and hence digestive processes are faster. This may be due to the higher SSTs at our study site (27 – 34°C) compared to the other locations (24 – 28°C for the GBR and 27°C for Hawaii). In spite of higher bite rates, the estimated daily ingestion of grazed AFDM lies within the range of values reported for other parrotfishes (Bruggemann et al. 1994; Bruggemann et al. 1994a; Ferreira et al. 1998).

Seasonally varying bite rates in coral reef grazers are commonly reported (Polunin & Klumpp 1992; Ferreira et al. 1998; Hernaman et al. 2009). Parameters causing this variation in feeding rate are temperature, biomass, nutritional quality and productivity of turfs (Horn

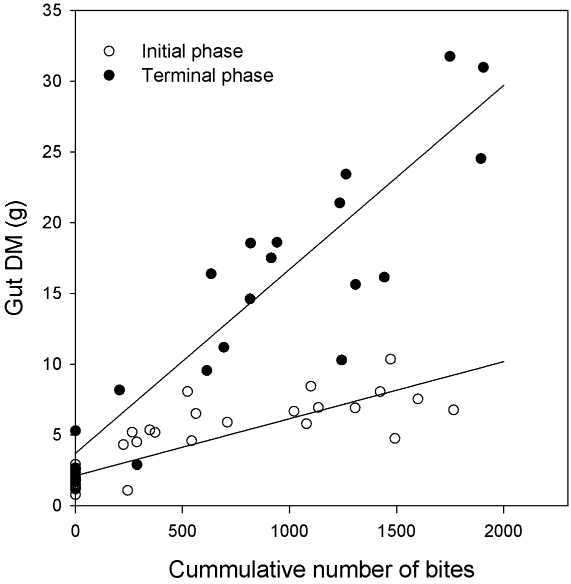

Fig. 4.6 Increment in gut dry mass (DM) as a function of cumulative number of bites for initial phase (IP, 20 – 25 cm forklength) and terminal phase (TP, 30 – 35 cm forklength) of *Scarus ferrugineus*.

& Gibson 1990; Bowen et al. 1995; Russ 2003; Clements et al. 2009). All these parameters vary seasonally at our study site. EAM biomass is lowest in the warmer seasons (Ateweberhan et al. 2006a, Fig. S4.2.1A), while its nutritional quality expressed as percentage organic matter of dry mass is highest during this period (Figs. S4.2.1B,C). Indeed high biomass turfs are associated with high sediment loads and hence represent poorer quality food (Purcell 2000; Purcell & Bellwood 2001; Bonaldo & Bellwood 2011). Also the productivity is expected to be higher in the warmer seasons since both the photosynthetically available radiation (PAR) and temperature – main parameters that affect primary productivity – are highest during this period (Ateweberhan et al. 2005a). It is therefore plausible that the higher bite rates in the warmer parts of the year for *S. ferrugineus* could be due to increased nutritional quality, higher productivity, higher temperatures or a combination of these. More experimental work is needed to separate the relative roles of these factors.

We did not analyse the dietary components of the material ingested by *S. ferrugineus*. However behavioural observations show that the species mainly targets the EAM (Afeworki et al. 2011). Detritus is an integral part of the EAM and its nutritional quality is comparable to or better than that of the algae (Crossman et al. 2001; Wilson et al. 2003). When parrotfishes take bites they include all the components of the EAM i.e. the detritus, the epilithic algae and the substrate bound endolithic algae (Bruggemann et al. 1994; Bruggemann et al. 1994a). Gut content of *S. ferrugineus* and other parrotfishes (Choat et al. 2002) typically is a triturated mass of sediment, algal fragments, and detritus, reflecting its EAM source. Indeed, dietary analyses have confirmed that parrotfishes of the genus *Scarus* and *Chlorurus* ingest large amounts of detritus (Choat et al. 2002; Choat et al. 2004).

Table 4.3 *Scarus ferrugineus*. Mean daily intake of epilithic algae community (±SE) by initial phase, terminal phase and territorial terminal phase individuals.

Period	20 – 25 cm IP		30 – 35 cm TP		30 – 35 cm TTP	
	g DM day^{-1}	g AFDM day^{-1}	g DM day^{-1}	g AFDM day^{-1}	g DM day^{-1}	g AFM day^{-1}
Feb – Mar	71.96 (6.16)	8.04 (2.84)	107.40 (15.51)	12.39 (5.99)	75.15 (12.39)	8.68 (4.26)
Apr – May	83.14 (8.02)	9.28 (3.31)	151.39 (20.39)	17.48 (8.39)	114.58 (18.40)	13.23 (6.48)
Jun – Jul	85.75 (7.87)	9.57 (3.40)	122.52 (15.67)	14.15 (6.75)	95.52 (13.43)	11.03 (5.32)
Aug – Sep	80.71 (7.00)	9.02 (3.19)	133.56 (17.72)	15.41 (7.39)	104.21 (13.63)	12.03 (5.76)
Oct – Nov	66.82 (5.81)	7.46 (2.64)	125.94 (19.45)	14.53 (7.08)	105.83 (14.40)	12.21 (5.86)

Varying levels of food intake are likely to influence life history decisions such as investment in reproduction and growth (Jones 1986; Clifton 1995; Berumen et al. 2005). In *S. ferrugineus*, the low intake rate during the cooler parts of the year coincides with near zero growth rates, low body condition and declining liver mass indices (Chapters 5; 7). Low daily bite rates during the cool season are possibly due to a combination of low temperature (see below), the low abundance of the preferred food item (Afeworki et al. 2011), and possibly due to higher sediment load of turfs during this season (Fig. S4.2.1). As a result, the cool season represents a period of lower energetic and nutrient intake for this population of *S. ferrugineus* that may limit growth and reproduction. In contrast the temporal concordance of high nutritional quality EAM, high intake rates and high processing rates during the warm seasons, strongly suggests that *S. ferrugineus* is nutritionally and energetically better off in the warmer parts of year.

4.4.2 Size and bite rate

Bite rate follows a quadratic function with size and the peak values occur at intermediate sizes (Bruggemann et al. 1994, this study). By controlling for the role of territoriality (Table S4.3.1), our results clearly demonstrated that fish size, not life phase as such, determines bite rate. Size also affects the area scraped per bite (scraping capacity), being higher in larger than in smaller individuals (Bruggemann et al. 1996; Bonaldo & Bellwood 2008; Afeworki et al. 2011). Changes in the size structure of parrotfish populations, e.g. as a result of overfishing, will therefore affect the capacity of parrotfish to remove algae from coral substrates and the role of this functional group in maintaining reef resilience (Lokrantz et al. 2008; Jayewardene 2009).

Declining bite rate with size beyond the inflexion point (>15 cm) is compensated by the larger yield per bite leading to larger daily intake for these size classes (this study). For this part of the curve, the lower bite rates may be a direct result of the mechanics associated with bigger bites, analogous to the difference in bite rate between scrapers (who generally have high bite rates) and excavators (who take fewer but more forceful bites) (Bellwood & Choat 1990; Bruggemann et al. 1994a). Juveniles however have a smaller yield per bite (Bruggemann et al. 1994) and lower bite rate which may lead to lower daily intake in this group unless they target food items of higher nutritional quality, a phenomenon that is usually associated with lower feeding rates (Bruggemann et al. 1994; Bowen et al. 1995; Choat et al. 2004). It is possible that juveniles may target nutritionally better components of the epilithic algal community such as the meiofauna and/or detritus (Bellwood 1988; Bruggemann et al. 1994; Chen 2002).

4.4.3 Territorial behaviour and bite rate

During spawning, territorial males spend a large part of their time on non-foraging activities leading to a significant reduction in bite rates (Bruggemann et al. 1994; van Rooij 1996; Bonaldo et al. 2006). In *S. ferrugineus*, spawning-related losses in intake amount to 23% of the daily intake. This loss is exacerbated by the higher energy expenditure associated with territoriality. Indeed, spawning behaviour often involves increased swimming activity associated with agnostic encounters and territory defence (van Rooij 1996; Taborsky & Grantner 1998) which in turn affect growth and body condition of TTP (van Rooij et al. 1995b; van Rooij et al. 1995a). We have observed similar effects in *S. ferrugineus* where TP have higher mortality rates and shorter life spans than IP (Chapter 6). Energetic constraints associated with territoriality may partly explain this reduced survivorship in TP.

Another way in which spawning can interfere with food intake is due to the spatial disparity between spawning and foraging zones (Robertson 1991b; Kuwamura et al. 2009). Scarids, and reef grazers in general, typically forage in the highly productive shallow reef zones (Hay 1981a; Fox & Bellwood 2007; Brokovich et al. 2010). Spawning sites are normally located at deeper reef sites (van Rooij 1996). The importance of shallow reef areas for foraging parrotfishes is reflected in the tendency of many species to commute between shallow foraging and deeper spawning locations (Colin 1978; Johannes 1978; Kuwamura et al. 2009). A similar condition exists in *S. ferrugineus* where TTP migrate to the spawning sites located at the deep fore reef. At the end of each spawning episode the TTP swim back to the reef crest where most of the foraging activity occurs.

4.4.4 Temperature and bite rate

The relationship between feeding rate and temperature in fish follows a dome shaped curve where high temperatures cause a decline in feeding rate (Jobling 1994; Koskela et al. 1997). This is associated with the decline in aerobic scope of marine organisms at high temperatures due to the incapacity of the circulatory and ventilatory systems to cope with the high oxygen demand (Frederich & Pörtner 2000; Pörtner & Knust 2007; Nilsson et al. 2009). This effect is more pronounced in large than in small individuals (Hernandez et al. 2002; Peck et al. 2009; Morita et al. 2010). Consequently, fish populations will be composed of smaller individuals in warmer conditions (Daufresne et al. 2009). Our results suggest that, at our study site, the larger size class of *S. ferrugineus* is close to its upper critical temperature during the summer months. This is corroborated by previous studies at our site that pointed out a possible temperature mediated suppression of grazing during summer in the hot shallow zones leading to a shift in grazing intensity to the deeper and cooler reef zones (Ateweberhan et al. 2006a; Afeworki et al. 2013).

Summer SSTs at our study site at 2 m depth ranged from 32 – 34°C, while on the reef flats they often exceeded 36°C (Ateweberhan et al. 2005a; Ateweberhan et al. 2006a). These SSTs are equal to or higher than those reported as critical temperatures for some coral reef fishes (Mora & Ospina 2001; Ospina & Mora 2004; Nilsson et al. 2009). Our results suggest that such high temperatures are likely to negatively affect large parrotfishes first which, over time, may lead to reductions in size structure of the population.

The link between temperature and body size likely represents a critical mechanism by which global warming could alter the grazing function on coral reefs. Body size is a critical determinant of the ecological role of parrotfishes, such as grazing impact and bioeroding capacity, both of which increase exponentially with size (Bruggemann et al. 1996; Bonaldo & Bellwood 2008; Lokrantz et al. 2008; Bellwood et al. 2012). It has been noted that overfishing, by extirpating large parrotfishes, greatly impairs the resilience of coral reefs (Bonaldo & Bellwood 2008; Lokrantz et al. 2009; Bellwood et al. 2012). By protecting large herbivores from overfishing, grazing and hence the potential for recovery of corals after disturbance is enhanced in marine protected areas (Mumby et al. 2006; Mumby et al. 2007). Unlike overfishing, global warming could affect parrotfish communities on large spatial scales. Many reefs can be expected to experience changes in the size structure of fish populations, leading to communities that are dominated by smaller individuals and species. This will particularly be severe in locations subject to rapid warming (McClanahan et al. 2009a; Sherman et al. 2009; Raitsos et al. 2011) or those that already experience extreme summer temperatures, such as the southern Red Sea and the Persian Gulf (Kleypas et al. 1999a; Coles 2003; Ateweberhan et al. 2006a). If indeed global warming leads to reefs that are dominated by smaller individuals, the resulting reduction in grazing impact by parrotfishes may compromise their role in maintaining the resilience capacity of coral reefs.

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A4 Appendix

A4.1 Intake rate and body size

To develop a model for the relationship between body mass and intake rate of coral reef grazing fish, we collected intake rate estimates from the literature (Table A4.1.1). For the studies where intake rate is given in g ash free dry mass (AFDM) day^{-1} or in g dry mass day^{-1}, the values were converted into g Carbon day^{-1} using a conversion factor of 40.5% (Bruggemann et al. 1994) and 38% (Klumpp & Polunin 1990) respectively. In some studies intake rates were estimated for different size classes of the same species (Bruggemann et al. 1994; Bruggemann et al. 1994a). These were taken as individual data points. When intake rates were estimated at different reef zones (Bruggemann et al. 1994) or seasons (Polunin & Klumpp 1992), the mean values were taken. Parameters of the relationship between intake rate and body size were estimated in SPSS. The data for *Acanthurus lineatus* was an outlier and was not included in the final regression analysis.

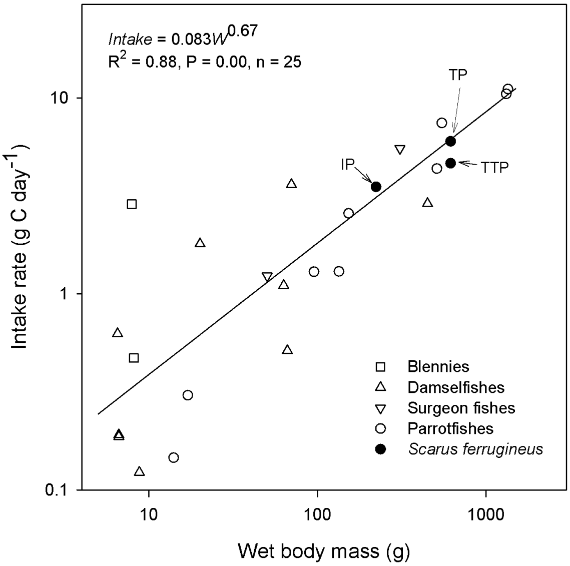

Fig. A4.1.1 Log-Log plot of daily intake rate (g C day^{-1}) of epilithic algae and wet body mass (W) of coral reef grazing taxa. Also shown is the best fit regression line. Values for different grazing taxa from the literature. IP: 20 – 25 cm initial phase; TP: 30 – 35 cm terminal phase; TTP: 30 – 35 cm territorial TP. Note that territorial TP of *S. ferrugineus* ingest lower than expected for their mass.

The mass exponent of the relationship between intake rate and body mass is 0.67 (Fig. A4.1.1). Estimates of this scaling exponent usually range between 0.7 and 1 for many fish species (Cui & Liu 1990a; Bruggemann et al. 1994). This is comparable to the scaling exponent of body mass to metabolic rate in ectothermic organisms which ranges between 0.67 and 1 (Jobling 1988; Cui & Liu 1990b). Higher mass specific consumption rate in smaller fish therefore appears to be due to their higher mass specific metabolic rates. Our estimates for *S. ferrugineus* are comparable to those of similar sized scarids.

Table A4.1.1 Estimates of intake rate in g Carbon day^{-1} of herbivorous fishes.

Family	Species	Size (cm)	Wet body mass	Intake g Carbon day^{-1}	Source
Blennies (Blenniidae)	*Salarias fasciatus*	8.5	8.119	0.471^{a}	Klumpp & Polunin 1990
	Salarias fasciatus	9.2	7.9	2.867	Townsend & Tibbetts 2004
Damselfish (Pomacentridae)	*Microspathodon dorsalis*	21.0	450	2.888	Montgomery 1980
	Plectroglyphidodon lacrymatus	6.27	6.509	0.626	Polunin 1988
	Pomacentrus chrysurus	6.0	6.617	0.191^{a}	Polunin & Klumpp 1992
	Pomacentrus flavicauda	6.0	6.617	0.187^{a}	Klumpp & Polunin 1990
	Pomacentrus wardi	7.2	8.76	0.123	Townsend & Tibbetts 2004
	Stegastes apicalis	11.2	63	1.103 ^{a}	Klumpp & Polunin 1989
	Stegastes fuscus	13.5	66.255	0.513	Ferreira et al. 1998
	Stegastes nigricans	8.0	20.074	1.799	Letourneur et al. 1997
	Stegastes rectifraenum	10.0	70.0	3.610	Montgomery 1980
Parrotfish (Labridae)	*Scarus ferrugineus*	22.5	222.641	3.514^{a}	This study
	Scarus ferrugineus	32.5	616.562	5.992^{a}	
	Scarus ferrugineus	32.5	616.562	4.632^{a}	
	Scarus vetula	10.0	14.0	0.146	Bruggemann et al. 1994b
	Scarus vetula	20.0	134.0	1.300	
	Scarus vetula	30.0	511.0	4.349	
	Scarus vetula	40.0	1320.0	10.469	
	Sparisoma viride	10.0	17.0	0.304^{b}	Bruggemann et al. 1994a
	Sparisoma viride	20.0	153.0	2.572^{b}	
	Sparisoma viride	30.0	547.0	7.438^{b}	
	Sparisoma viride	40.0	1350.0	11.074^{b}	
	Sparisoma atomarium	19.3	95.286	1.296^{a}	Ferreira et al. 1998
Surgeonfish (Acanthuridae)	*Acanthurus bahianus*	24.2	308.861	5.519^{a}	Ferreira et al. 1998
	Acanthurus lineatus	22.9	331.112	10.900^{a}	Polunin & Klumpp 1992
	Acanthurus nigrofuscus	12.2	50.326	1.236	Montgomery et al. 1989

[a] Mean of seasonal estimates of intake rate

[b] Mean of intake rates estimated at different reef zones

S4 Supplementary Material

S4.1 Sampling periods

Alternating cool and hot seasons in the southern Red Sea are driven by the Indian Ocean monsoon system. The cool season extends from December through March, while the hot season lasts from May to October (Ateweberhan et al. 2005a; Ateweberhan et al. 2006a). Transition periods between these seasons are characterized by variable wind patterns and intermediate temperatures. Mean monthly sea water temperatures at 2 m depth at the study site range from 27.0 to 33.4°C (Ateweberhan et al. 2006a, Fig. S4.1.1). The bite rate sampling periods were selected to encompass the entire annual temperature range (Fig. S4.1.1). Samples for quantifying the yield per bite were collected during two periods with contrasting temperatures (Fig. S4.1.1). Yield per bite and dawn-to-dusk defecation rates were also determined during these two periods.

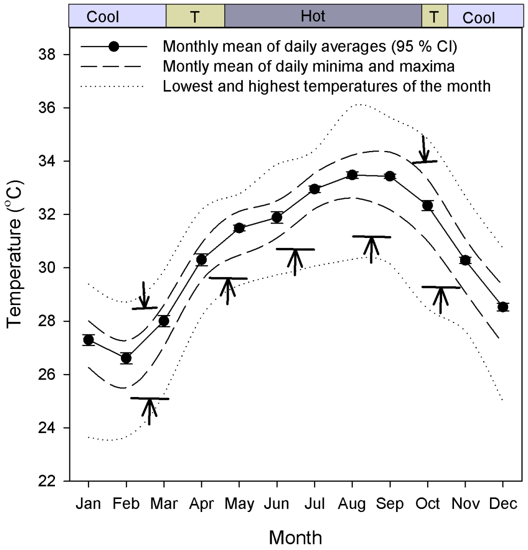

Fig. S4.1.1 Monthly variation in seawater temperature at the study site (2003 – 2006). The cool season, associated to the SW monsoon, and the hot season during the NE monsoon are shown. T = transition periods with variable wind directions. Upward pointing arrows indicate sampling periods where bite rates were recorded. Downward pointing arrows represent periods during which yield per bite and dawn-to-dusk defecation rate were recorded.

S4.2 Turf biomass and ash free dry mass (AFDM)

Turf algae biomass was assessed from natural carbonate substrates between 2007 and 2008 at the reef crest, on the shallow fore reef and the deep fore reef during February, April, September and December. At least four dead coral substrates covered by turf algae (100% cover) were selected haphazardly. From each of these substrates a piece was chiseled off and kept in a separate plastic bag during transport to the lab. Turfs were carefully removed using a scalpel, taking care not to include substrate bound endolithic algae. A piece of aluminum foil of known areal density was modeled over the substrate and carefully trimmed to match the irregular edges of the coral piece. The surface area was then estimated by dividing the weight of the piece by the density per unit area of the aluminum foil. To determine the ash free dry mass, samples were dried at 60°C, and ashed at 550°C in a muffle furnace for 8.5 hours.

Biomass of turfs at the reef crest and on the shallow fore reef (the two main foraging zones of *S. ferrugineus*) is highest during the cool season. The percentage AFDM is negatively correlated with turf biomass (Fig S4.2.1C). The cover and biomass of turf algae at our study site show opposing seasonal trends: turf biomass is highest and its cover lowest during the cool season (Ateweberhan et al. 2006a; Afeworki et al. 2011).The fact that low biomass turfs cover much of the dead coral surface in spring and summer suggests that the availability of better nutritional quality food is higher during these periods. Indeed detailed analyses of the nutritional value of the epilithic algal matrix (EAM) on the Great Barrier Reef show that the nutritional value of EAM is inversely proportional to its biomass (Purcell 2000; Purcell & Bellwood 2001; Bonaldo & Bellwood 2011), as high biomass turfs tend to contain more sediment and hence are of poor nutritional quality. In addition, there is a positive correlation between the percentage AFDM and the percentage protein content in marine algae (Bolser & Hay 1996). Given this,

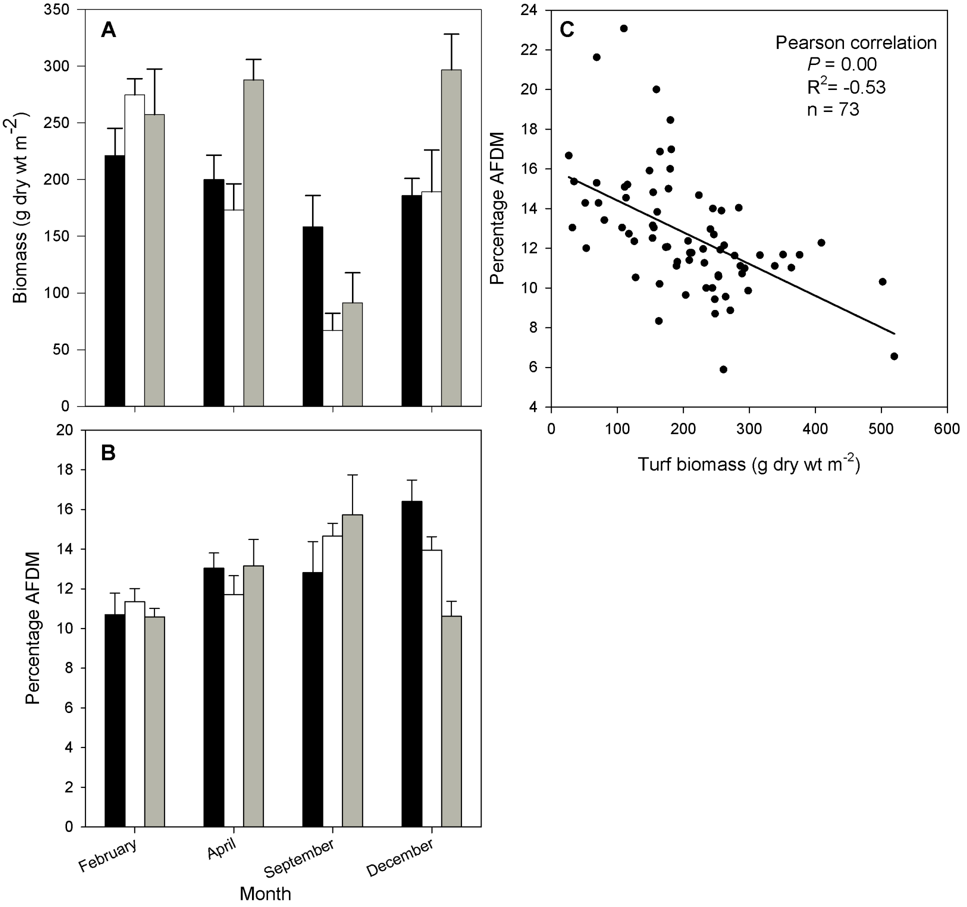

Fig. S4.2.1 Seasonal trends in mean (±SE) biomass (A) and percentage ash free dry mass (AFDM) (B) of epilithic algal matrix (EAM) from three reef zones of the fringing reef at Sheikh Said Island. (C) Relationship between percentage ash free dry mass (AFDM) and biomass of EAM.

the percentage AFDM provides an indication of the nutritional quality of turfs (Bolser & Hay 1996; Wilson 2002).

S4.3 Fish size, life phase and bite rate

Effect of life phase on bite rate: The objective was to quantify bite rate and intake rate for the three main size/social categories of *Scarus ferrugineus*: 20 – 25 cm initial phase (IP), 30 – 35 cm terminal phase (TP) and 30 – 35 cm territorial TP. However, bite rate differences between 20 –

25 cm IP and 30 – 35 cm TP could be related both to size (Bruggemann et al. 1996; Lokrantz et al. 2008) and social status (Bruggemann et al. 1994; van Rooij et al. 1996; Bonaldo et al. 2006). To differentiate between these two factors, an additional data set of bite rates was collected for TP whose size overlaps with that of the IP. While testing the effect of size and/or life phase on bite rate, data of territorial TP was excluded. Thus, the results reflect the effect of size and/or life phase on bite rate and not of territoriality. Analysis of covariance (ANCOVA) was conducted for each period with bite rate as a dependent variable, life phase as factor and size as covariate. Prior to conducting ANCOVA tests data was tested for normality and homogeneity of variance using the Explore procedure in SPSS. In the size class where IP and TP overlap bite rate did not differ between the two (Table S4.3.1).

Table S4.3.1 *Scarus ferrugineus*: summary of ANCOVA results comparing bite rate (bites min^{-1}) between IP and TP fish of 20 – 25 cm fork length. Significant effects are shown in bold.

Period	Source	SS	*df*	MS	*F*	*P*
Feb – Mar	Life phase	98.881	1	98.881	1.388	0.248
	Size	12.899	1	12.899	0.181	0.674
	Life phase * Size	91.201	1	91.201	1.280	0.267
	Error	2137.717	30	71.257		
Jun – Jul	Life phase	10.761	1	10.761	0.191	0.668
	Size	164.719	1	164.719	2.925	0.108
	Life phase * Size	10.130	1	10.130	0.180	0.677
	Error	844.703	15	56.314		
Aug – Sep	Life phase	7.176	1	7.176	0.112	0.739
	Size	93.097	1	93.097	1.456	0.232
	Life phase * Size	0.099	1	0.099	0.002	0.969
	Error	4412.881	69	63.955		
Oct – Nov	Life phase	0.703	1	0.703	0.018	0.893
	Size	160.345	1	160.345	4.212	**0.047**
	Life phase * Size	3.485	1	3.485	0.092	0.764
	Error	1560.663	41	38.065		

Effect of size on bite rate: To fully investigate the relationship between size and bite rate, additional data was collected for sizes outside of the target group (namely <20 cm and 25 – 30 cm fork length). Since small individuals (5 – 10 cm) are abundant during the summer months, bite rate data for this category was collected mainly during the June – July and August – September sampling periods. As a result, bite rate data for the widest size range of *S. ferrugineus* was available during these two periods only. Bite rate data of IP and TP was pooled since there is no significant effect of life phase (see above). Data from TTP was however excluded. ANCOVA tests showed that the mean bite rate did not differ between June – July and August – September (ANCOVA: period: $P = 0.311$, $F = 1.033$, size: $P = 0.000$, $F = 50.030$, n =197). In consequence, data from these two periods was pooled to generate a best fitting model relating bite rate and fish size using the curve fitting procedures in SPSS. A quadratic function was selected as the best fitting model based on the R^2 values. All data analysis was done in SPSS for Windows 16 (2007).

CHAPTER 5

SEASONAL AND LIFE-PHASE RELATED DIFFERENCES IN GROWTH IN THE PARROTFISH *SCARUS FERRUGINEUS* ON A SOUTHERN RED SEA FRINGING REEF

Y. Afeworki, J. J. Videler, Y. H. Berhane, & J. H. Bruggemann

Abstract Temporal trends in growth of the rusty parrotfish *Scarus ferrugineus* were studied on a southern Red Sea fringing reef that experiences seasonal changes in environmental conditions and benthic algal resources. Length increment data from tagging and recapture was compared among periods/sexes and modelled using GROTAG – a von Bertalanffy growth model. The growth pattern of *S. ferrugineus* is highly seasonal with a maximum occurring between April and June and a minimum between December and March. Body condition tracks the seasonal variation in growth, increasing from April – June and decreasing from December – March. The season of maximum growth coincides with high irradiation, temperature increases and peak abundance of the primary food source: epilithic algal community. There is a decline in growth rate during summer (July – October) due to a combination of extreme temperatures and lowered food availability. There was strong sexual dimorphism in size (SSD) and life history traits. Terminal-phase males (TP) achieve larger asymptotic lengths than initial-phase individuals (IP) (L_∞: 34.55 cm vs 25.12 cm) with growth coefficients (K) of 0.26 and 0.38 respectively. The TP were growing 4 times as fast as IP of similar size. Three individuals changed status (IP to TP) while at liberty and grew 8 times faster than IP of similar size suggesting that sex change in *S. ferrugineus* is accompanied by a surge in growth rate. The SSD in *S. ferrugineus* thus coincides with fast growth that starts during sex change and continues into the terminal phase. Faster growth during sex change suggests that the cost associated with sex change is limited and that deferral of reproduction during the transitional period results in increased growth.

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5.1 Introduction

Grazing activities on coral reefs significantly impact the benthic algal communities (Wanders 1977; Hatcher & Larkum 1983; Williams & Polunin 2001; Stockwell et al. 2009). Grazer biomass in coral reefs may be limited by turf productivity (Klumpp & Polunin 1990; Russ & McCook 1999). This is supported by the tendency of fish grazers to increase their abundance, feeding rates or growth rates following increases in food availability due to coral mass mortality (Hart & Russ 1996; Garpe et al. 2006; Adam et al. 2011) or competitor removal, e.g., following the mass mortality of *Diadema antillarum* in the Caribbean (Carpenter 1988; Carpenter 1990; Robertson 1991a) or after experimental removal of sea urchins (Hay & Taylor 1985; McClanahan et al. 1994; McClanahan et al. 1996).

One way in which resource limitation can affect population size is by limiting individual growth and body condition both of which directly or indirectly influence reproductive output (Schultz & Warner 1991; Bohlin et al. 1994; Jorgensen et al. 2006; Grift et al. 2007). A number of studies have indeed demonstrated that increases in food supply promote higher growth rates, better body condition and increased reproductive output in coral reef fishes (Jones 1986; Anderson & Sabado 1995; Clifton 1995; Berumen et al. 2005; Kingsford & Hughes 2005). Temporally or spatially varying levels of resources can also be expected to influence population processes in reef fishes (Jones & McCormick 2002).

In temperate and subtropical environments, the seasonally varying environmental parameters, such as light intensity and temperature, are known to drive seasonal cycles of growth and reproduction in primary and secondary producers (Horn et al. 1986; Coma et al. 2000). Many coral reef areas show similar albeit less dramatic seasonal changes in environmental conditions (McClanahan 1988). These are often associated with significant changes in the community structure, abundance, nutritional quality and productivity of benthic algae (Carpenter 1985; Klumpp & Mckinnon 1989; Diaz-Pulido & Garzon-Ferreira 2002; Ateweberhan et al. 2006a). The bite and intake rates or food preferences of herbivores often show parallel changes (Letourneur et al. 1997; Ferreira et al. 1998; Afeworki et al. 2011; Lefevre & Bellwood 2011). These are likely to alter energy budgets, resulting in growth and reproduction variations in reef associated grazers. In this study we make use of the highly seasonal environment of the southern Red Sea to investigate how variation in resources and temperature influence the rusty parrotfish *Scarus ferrugineus*.

Extreme summer temperatures strongly affect coral reef algal communities in the southern Red Sea (Ateweberhan et al. 2006a; Afeworki et al. 2011). Large biomass of canopy forming and foliose macroalgae builds up and crustose corallines prevail in the shallow reef zones during the cooler part of the year (Ateweberhan et al. 2005a; Ateweberhan et al. 2005b; Ateweberhan et al. 2006b). In contrast, turf algae attain highest cover during the hottest months (Ateweberhan et al. 2006a; Afeworki et al. 2011). Throughout the year, *S. ferrugineus* feeds exclusively on algal turfs and associated biota, with a strong preference for turfs growing on substrates with endolithic algae (Afeworki et al. 2011). During the cool season, *S. ferrugineus* augments its diet with turfs associated with crustose corallines to compensate for the decline of its preferred food source. Moreover the daily intake rate is lowest during the cool period (Afeworki et al. 2013). Here we examine the effect of these seasonal changes on the somatic growth *S. ferrugineus* – a dominant grazer – on a southern Red Sea fringing reef.

5.2 Methods

5.2.1 Study site and study species

The study was conducted on the gently sloping fringing reef of Sheik Said Island (15°35′N; 39°29′E), Massawa, Eritrea. Despite its inshore location and proximity to the port city of Massawa, the reef has high (30 – 50%) coral cover (Zekeria & Videler 2000; Afeworki et al. 2011) and supports a diverse and abundant grazer community (Afeworki et al. 2013). There is a low intensity, canoe based, fishery around Massawa, but parrotfishes or other reef grazers are not targeted (Tsehaye et al. 2007).

The area experiences two distinct monsoon associated seasons, the cool (mean temperature 27.7°C) season from December to March and a hot (mean temperature 33.4°C) season from May to October (Morcos 1970; Edwards 1987; Ateweberhan et al. 2006a). The cool season is further characterised by high cloud cover, low light levels, high wind speeds and higher rainfall (Ateweberhan et al. 2005a). The transition periods between these two seasons are brief and are characterized by variable wind patterns. Benthic algae, corals and fish are greatly affected by the seasonal changes in environmental conditions (Guillaume et al. 2000; Ateweberhan et al. 2006a; Zekeria et al. 2006). The seasonal fluctuations in the biomass and composition of benthic algae are of particular relevance to grazing animals (Ateweberhan 2004).

The rusty parrotfish, *S. ferrugineus*, is common and endemic to the Red Sea and the Arabian Gulf (Randall 1983). At our study site it is the dominant grazer, representing 34% of the total grazer biomass (Afeworki et al. 2013). *S. ferrugineus*, like most parrotfishes, is a diandric protogynous hermaphrodite (Abdel-Aziz et al. 2012). The initial-phase individuals (IP) are mainly females (~5% being males), attain a maximum fork length of 26 cm and have a brown to yellowish coloration. Terminal-phase individuals (TP) are males, reach 36 cm and are brightly coloured blue, green, and yellow. Individuals in the process of changing sex have an intermediate colouration and are identified as transitional phase fish (TIP).

5.2.2 Tagging and recapture

Fish tagging was conducted between January 2006 and January 2008, following a monthly sampling schedule. Fish were caught with scoop nets after driving them into barrier nets, mostly between 1730 – 1830 hrs, after feeding activity ceased, when fish are migrating to their sleeping ground. To ensure gut evacuation, fish were kept overnight in perforated plastic barrels. The next day, fish were anaesthetized in a bucket of seawater with a few drops of clove oil based water soluble anaesthetic AQUI-S (AQUI-S Ltd, Lower Hutt, NZ). Excess water from gills was squeezed out and the rest of the body dried by wrapping the fish in a humid towel and gently dabbing the fish. Subsequently, the fork length (to the nearest mm), wet mass (to the nearest 0.1 g), life phase and the date of capture were recorded. Each individual was then tagged with a visible alphanumeric implant tag (Northwest Marine Technology, Inc) placed in the tissue between two anal fin rays. After processing, fish were allowed to recover in drum nets before being released at the site of capture. Data were collected during three periods: December – March, corresponding to the cool season; April – June, a period of rising temperatures; July – October, the period with the highest temperatures of the year. The length increment of fish that were captured, tagged and recaptured within each period was taken to represent growth during that particular period. The growth increment of individuals that were recaptured after >150 days was considered to represent annual growth.

5.2.3 Comparison of growth rates

The specific growth rate G (Jobling 1994) was calculated using:

$$G = 100 * \frac{lnL_2 - lnL_1}{t_2 + t_1} \tag{5.1}$$

where L_1 is the initial fork length (cm) at time t_1 and L_2 the fork length at recapture (time t_2). Specific growth rates among periods and life phases (IP, TP, and TIP) were compared using ANCOVA with growth rate as dependent variable, season or life phase as factors and length as covariate. Tests were limited to the 20 – 25 cm size class for which sufficient recaptures were made. When differences were significant, multiple comparisons were undertaken using pair wise contrasts with Bonferroni correction for multiple comparisons. Length and weight data was linearized by log-transformation and monthly variation in wet mass, was tested using analysis of covariance (ANCOVA) with weight as a dependent variable, month as factor and length as the covariate. Henceforth the term "body condition" will be used to refer to the length specific wet mass of individuals. Prior to analysis, data was tested for normality and equality of variances. The log-transformed data of wet mass conformed to the requirements of ANCOVA test. Annual growth data of IP, TIP and TP were not normal and variances were unequal. Comparison of annual growth between the sexes was therefore conducted on square root transformed data that achieved normality and homescedasticity. Seasonal growth data did not violate equality of variances and normality except the July – October data for IP which was not normal. As data transformations did not achieve normality, ANCOVA was conducted on untransformed data, as suggested by (Underwood 1997).

In addition to the comparison at the selected length class we also modelled growth using GROTAG, a reparametrized version of the von Bertalanffy growth function for tagging data (Equation 5.2) (Francis 1988a). Instead of the standard von Bertalanffy (VBFG) parameters, GROTAG uses two growth rate parameters g_α and g_β which are the mean annual growth rates of fish of lengths α and β. The lengths α and β are selected in such a way that they are well represented in the tagging data. This renders these two parameters direct estimates of growth rate from the data, rather than being mathematical constructs as L_∞ and K are (Francis 1988b). Moreover, these parameters show low correlation and have desirable statistical qualities that allow comparative studies (Francis 1988a).

Table 5.1 *Scarus ferrugineus*. Sample sizes of each life phase recaptured during the study and the period of their capture.

Sampling Periods	Life phase			
	IP	TIP	TP	Total
Annual	19	1	6	26
Apr – Jun	5	1	0	6
Jul – Oct	15	0	7	22
Dec – Mar	7	1	3	11
Total	46	3	16	65

GROTAG further includes two parameters (μ and ω) for describing seasonality in growth rates, where ω describes the time of year (relative to January 1) where maximum growth occurs, while μ describes the amplitude of the seasonality. The value of μ ranges between 0 implying no seasonality and 1 indicating a maximum seasonal growth effect. The latter signifies that growth ceases at some point in the year. The model also incorporates parameters for measurement error with a mean of m and standard deviation of s and another for estimating the proportion of outliers in the data p.

$$\Delta L = \left[\frac{\beta g_\alpha - \alpha g_\beta}{g_\alpha - g_\beta} - L_1\right]\left[1 - \left(1 + \frac{g_\alpha - g_\beta}{\alpha - \beta}\right)^{\Delta T + (\Phi_2 - \Phi_1)}\right], \tag{5.2}$$

where $\Phi_i = \mu \frac{\sin[2\pi(T_i - \omega)]}{2\pi}$, for $i = 1, 2$.

The data set required to fit GROTAG are L_1 (initial length), ΔL (length increment), and T_1 (time at first release) and T_1 (time at recapture). Dates were expressed as fractions of the year starting from 1st January 2006 ($T = 0$). The model was fitted by maximizing the log-likelihood function (λ) (Equation 5.3) for a data set with $i = 1$ to n growth increment observations.

$$\lambda = \sum_{i=1}^{n} ln\left[(1 - p)\lambda_i + \frac{p}{R}\right], \tag{5.3}$$

where $\lambda_i = \exp \frac{-1/2(\Delta L_i - \mu_i - m)^2/(\sigma_i^2 + s^2)}{\left[2\pi(\sigma_i^2 + s^2)\right]^{1/2}}$. and μ_i is the expected value of growth increment (estimated by Equation 5.2) of the $i^{t}h$ individual with a standard deviation of σ_i. In this study we assume σ_i to be proportional to μ_i (i.e. $\sigma_i = \upsilon\mu_i$) (Francis 1988a) where the parameter υ describes the scaling factor of individual growth variability. The mean annual growth at any other length γ was estimated with Equation 5.4 (Francis 1988a) and their standard error was estimated using the delta method.

$$g_\gamma = \frac{\left((\gamma - \alpha)g_\beta + (\beta - \gamma)g_\alpha\right)}{(\beta - \alpha)}, \tag{5.4}$$

GROTAG growth parameters are related to the standard von Bertalanffy growth parameters by the following (Francis 1988b):

$$L_\infty = \frac{(\beta g_\alpha - \alpha g_\beta)}{(g_\alpha - g_\beta)}, \tag{5.5}$$

$$K = -\ln\left(1 + \left(\frac{(g_\alpha - g_\beta)}{(\alpha - \beta)}\right)\right), \tag{5.6}$$

where L_∞ is the asymptotic length or the average length of the oldest fish and K is the coefficient of growth or the rate at which L_∞ is reached. A stepwise fitting procedure was employed as suggested by Francis (1988a) using the Fish Methods package in the freely available statistical package R (R development team). Initially a three parameter model was fitted (Model 1 in Table 5.1). Additional parameters were included sequentially, depending on their impact on the value of the negative log-likelihood (NLL) and on the Akaike Information Criterion (AIC). Those that reduced the NLL the most were included first. Significance of an added parameter was evaluated by likelihood ratio test, whereby a parameter was considered significant if it reduced the NLL by at least 1.96 (Francis 1988a). The model that gave the lowest AIC and NLL value was finally selected as the best fitting one.

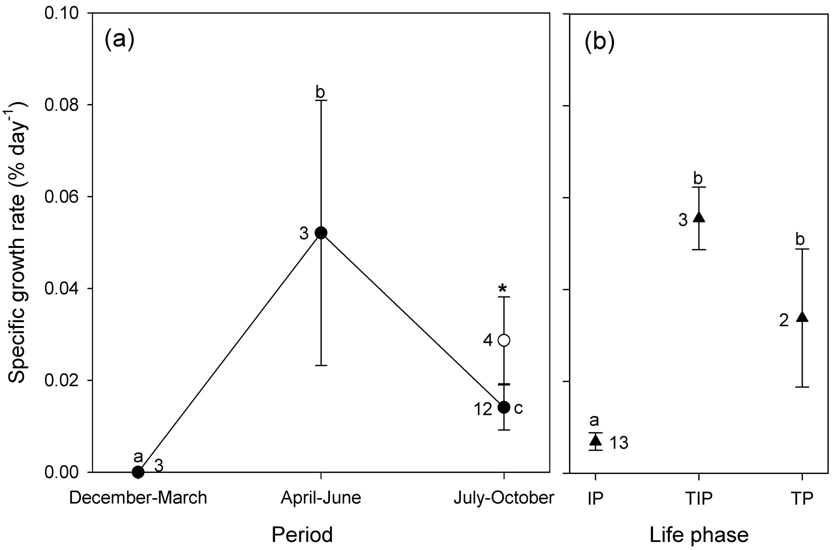

Fig. 5.1 *Scarus ferrugineus*. Specific growth rates (mean ±SE) of 20 – 25 cm fork length fish. (A) Within year variation in specific growth rates of IP. For comparison, the mean growth rate of TP is given for the July – October period. The asterisk indicates a significant difference in growth rates between IP and TP. (B) Mean annual specific growth rates of IP, TP and TIP. Significant differences are indicated by different letters.

5.3 Results

A total of 650 fish were tagged during the study, of which 65 were recaptured. Times at liberty ranged from 6 to 485 days. Only those individuals which were recaptured at least 25 days after release were used for further analysis. This criterion implied that we were able to include 45 IP, 16 TP and 3 TIP (showing complete transformation from IP to TP while at liberty) (Table 5.1).

Table 5.2 *Scarus ferrugineus*: Summary of ANCOVA tests of the monthly trends in wet body mass of initial phase and terminal phase fish with empty guts. Significant values in Bold.

Factor	Initial phase			Terminal phase		
	df	*F*	*P*	*df*	*F*	*P*
Intercept	1	1298.95	**0.00**	1	254.54	**0.00**
Fork length	1	7353.34	**0.00**	1	1479.43	**0.00**
Month	9, 247	13.00	**0.00**	7,55	3.24	**0.01**

IP between 20 – 25 cm fork length showed significant growth difference among periods (ANCOVA: period: $F_{2,18}$ = 18.98, P = 0.000) (Fig. 5.1A). The growth rate varied from a maximum during April – June to a minimum (zero growth) during the cool December – March period. Clearly the bulk of the annual growth in IP happens during the warmer parts of the year (Figs. 5.1A, B). Pairwise comparisons between seasons indicated that the mean growth rates are significantly different among periods (P values 0.00 – 0.01). For TP comparison among the periods was not possible, because multiple records were obtained only for the July – October period (Table 5.1). During this period the growth rate was about twice that of IP (ANCOVA: life phase: $F_{2,16}$ = 12.03, P = 0.004) (Fig. 5.1A). Only one TP of 20 – 25cm size range was sampled during the December – March period and its growth rate was zero, which is equivalent to that of the IP sampled during the same season.

Comparison of the annual growth of IP, TP and the three TIP indicated significant differences in growth rates (ANCOVA: life phase: $F_{2,18}$ = 28.89, P = 0.000). Pairwise comparison suggests that growth rate of IP is significantly lower than that of both the TIP (P = 0.000) and TP (P = 0.001). Although TIP had on average higher growth rates compared to TP the difference was not significant (P = 0.497) (Fig. 5.1B).

Analysis of body condition is based on the wet mass of 322 individuals with empty guts recorded during the tagging operations. Body condition of IPs and TPs varied seasonally (Table 5.2) and was lowest during March and April (Fig. 5.2C). From April onwards, body condition increases reaching maximum values during October to December. The maximum rate of increase in wet mass occurred from April – June, a period which coincides with the maximum length growth in IPs (Fig. 5.2C).

5.3.1 GROTAG growth model

GROTAG gave a good fit to the tagging data of *S. ferrugineus*. Based on the NLL and the AIC values, a six parameter model (Table 5.3; Model 6) was selected as the best fitting for IP. The introduction of the two parameters describing seasonality (μ, ω) resulted in substantial reduction on the NLL and AIC (see Table 5.3) indicating that growth in *S. ferrugineus* is highly seasonal. The season of peak growth (ω = 0.46) occurs around June. The amplitude of seasonal growth (μ = 1) suggests that growth in IP virtually ceases during the cooler part of the year (Fig. 5.1 and Fig. 5.2C). For TP a four parameter model gave the best fit (Table 5.3, Model 2). Introduction of the seasonality parameters did not improve the fit. This was probably due to the small sample size (16) and the absence of data for the season of peak growth (Table 5.1).

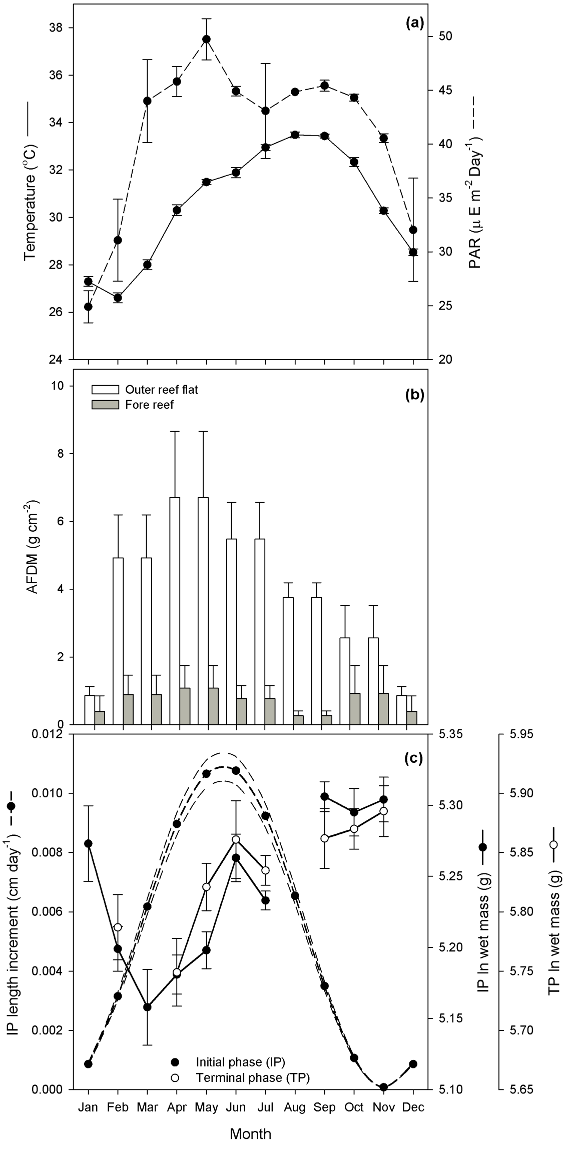

Fig. 5.2 *Scarus ferrugineus*. (A) Seasonal trends in photosynthetically available radiation (PAR) and water temperature on the study site (adapted from Afeworki et al. (2013)). (B) Mean monthly (±SD) ash-free dry mass (AFDM) of turf algae in randomly selected quadrants on two reef zones where *S. ferrugineus* primarily feeds on (adapted from bi-monthly samples of Ateweberhan et al. (2006a)). (C) Mean monthly wet mass of initial phase and terminal phase fish with empty guts, and predicted daily length increment of initial phase fish. Monthly means of wet mass are estimated for a 21 cm IP fish and a 26 cm TP from the ANCOVA model. Monthly means of the daily growth of initial phase individuals and confidence regions are generated by simulation using predicted parameters and error with a mean $m = 0$ and variance $v = 0.77$.

Lack of overlap in the confidence intervals of the growth rate at g_{24} cm indicates that there is significant growth rate difference between the IP and the TP (Table 5.3). Trajectories of the predicted growth of IP and TP show that TP grow significantly faster than IP of similar size (Fig. 5.3).

Table 5.3 Parameter estimates, negative log likelihood function values ($-\lambda$) and Akaike information criterion (AIC) of a subset of possible GROTAG models fitted to tagging data of initial phase (IP) and terminal phase (TP) *Scarus ferrugineus*. The optimal model for each life phase is indicated in bold type. Values in brackets are standard errors.

Life phase	Model	g_α	g_β	v	μ	ω (yr)	S (cm)	m (cm)	p	AIC	$-\lambda$
IP $\alpha = 20$ $\beta = 24$	1	1.88 (0.15)	0.34 (0.11)				0.43 (0.11)			59.40	26.70
	2	1.88 (0.22)	0.38 (0.05)	0.97 (0.17)			0.09 (0.03)			43.30	17.70
	3	1.30 (0.16)	0.33 (0.05)	0.59 (0.10)			0.10 (0.02)		0.13 (0.06)	35.20	12.60
	4	1.26 (0.17)	0.31 (0.06)	0.60 (0.10)			0.10 (0.02)	0.015 (0.03)	0.13 (0.11)	36.90	12.40
	5	1.61 (0.13)	0.35 (0.05)	0.69 (0.07)	1.00 (0.00)	0.46 (0.02)	0.08 (0.02)	-0.01 (0.03)	0.00 (0.00)	24.00	4.00
	6	**1.61** **(0.19)**	**0.35** **(0.05)**	**0.70** **(0.10)**	**1.00** **(0.31)**	**0.46** **(0.04)**	**0.08** **(0.02)**	**-0.01** **(0.03)**		**22.00**	**4.00**
TP $\alpha = 24$ $\beta = 28$	1	3.58 (0.35)	2.17 (0.33)				0.56 (0.10)			33.10	13.50
	2	**2.38** **(0.44)**	**1.48** **(0.27)**	**0.53** **(0.21)**			**0.19** **(0.06)**			**18.30**	**5.20**
	3	2.87 (0.68)	1.82 (0.46)	0.39 (0.19)			0.20 (0.06)	-0.11 (0.14)		19.60	4.80
	4	2.17 (0.80)	1.57 (0.57)	0.66 (0.22)	0.77 (0.62)	0.52 (0.11)	0.00 (0.03)	-0.06 (0.07)	0.00 (0.35)	21.10	2.50
	5	2.17 (0.54)	1.57 (0.44)	0.66 (0.22)	0.77 (0.58)	0.52 (0.10)	0.00 (0.03)	-0.06 (0.06)		19.10	2.50
	6	1.73 (0.49)	1.19 (0.31)	0.99 (0.35)	1.00 (0.49)	0.53 (0.05)	0.00 (0.07)			19.60	3.80

5.4 Discussion

This study reports a significant temporal as well as life phase related variation in growth rates of the parrotfish *S. ferrugineus*. The growth rates were highest for TIPs followed by TPs, while IPs had the lowest growth rates. Growth rate in IPs was highly seasonal, reaching a maximum between April and June. Lack of samples for some seasons precluded the detection of seasonality in growth in the TPs. Nevertheless, in periods for which data was available growth of TPs followed the same pattern to that of IPs. Also the body condition of TPs follows a pattern similar to that of the IPs, suggesting a similar seasonality in TPs and IPs. Higher L_∞ from tagging than from age based VBGF is to be expected, since age-based L_∞ is by definition the mean length of the oldest individuals, while GROTAG L_∞ is the maximum length achieved in the population (Francis 1988b). The resulting growth trajectories of IPs and TPs derived from both models (Fig. 5.4) fits the typical tropical fish growth curve i.e. a fast initial growth that reaches asymptotic size in the first few years of life (Choat et al. 1996; Choat & Robertson 2002; Zekeria et al. 2006). Below these results are discussed in the context of proximate environmental conditions and life history decisions.

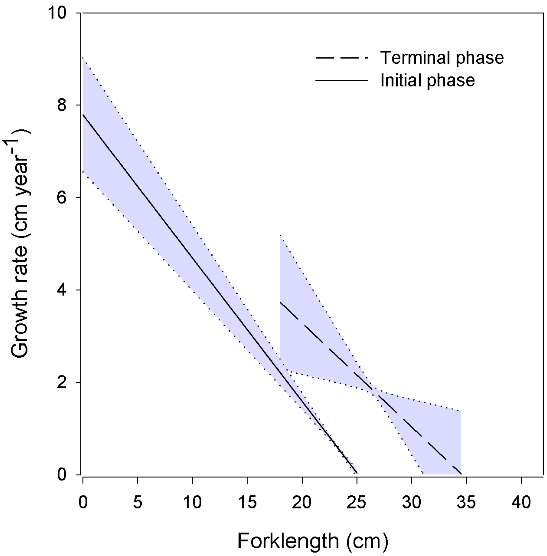

Fig. 5.3 *Scarus ferrugineus.* Predicted annual growth rates (±SE bands) for different initial lengths derived from the GROTAG model for two life phases. For the terminal phase growth predictions are made for sizes >18 since that is the minimum size observed for this life phase in this population.

5.4.1 The role of irradiance, temperature and resource availability in seasonal growth

Seasonality in growth and condition in *S. ferrugineus* is correlated with seasonal changes in irradiance, temperature and food availability (Fig. 5.2). Photosynthetically available radiation (PAR), temperature and food availability (epilithic algal community) vary substantially at our study site (Figs. 5.2A, B). The latter two are the primary environmental factors that affect growth of fishes. Higher temperatures during times of increased food availability typically lead to faster growth (Weatherley & Gill 1987; Jobling 1994). The period of highest growth and body weight gain is characterized by high (30 – 33°C) temperatures (Ateweberhan et al. 2006a; Afeworki et al. 2011). This period has higher abundance and better quality EAC (Afeworki et al. 2011; Afeworki et al. 2013) and the bite rate and food intake rate of *S. ferrugineus* peak during the same period (Afeworki et al. 2013). This strongly suggests that from April to June *S. ferrugineus* is able to acquire excess energy to fuel the observed growth and to store energy.

All life phases of *S. ferrugineus* feed on the EAC with strong preference for short turfs that grow on substrates with endolithic algae (Afeworki et al. 2011). The EAC is composed of filamentous algae, detritus and associated microfauna (Wilson et al. 2003). Parrotfishes are known to ingest substantial quantities of the detritus (Choat et al. 2002; Choat et al. 2004) and microfauna such as harpacticoid copepods (Kramer et al. 2013). The diet of *S. ferrugineus*

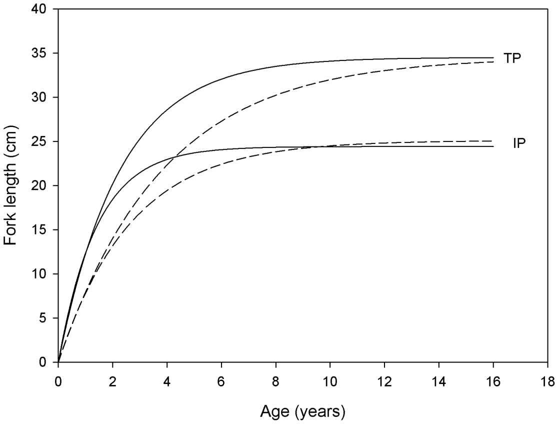

Fig. 5.4 *Scarus ferrugineus.* Growth of IP and TP predicted by the length-at-age based von Bertalanffy growth model (solid lines) and by the GROTAG model based on tagging data (dashed lines).

Table 5.4 *Scarus ferrugineus.* GROTAG estimates of the parameters of the von Bertalanffy growth function from tagging data compared to age-length derived parameters.

Life phase	L_∞		K	
	GROTAG	Length-at-age*	GROTAG	Length-at-age*
IP	25.12	24.43	0.38	0.70
TP	34.55	34.52	0.26	0.44

* von Bertalanffy parameters derived from length-at-age data (Chapter 6)

likely comprises all of these components of the EAC. The seasonal availability of these other components has not been studied. However, high quality detritus are expected to be more abundant during the warmer parts of the year, due to the high production of algal turfs and the massive die-off of canopy-forming macroalgae at the start of the hot season (Ateweberhan et al. 2005a; Ateweberhan et al. 2006b; Ateweberhan et al. 2006a). This massive shedding of thalli is estimated to add to the detritus load to nearby coral reef habitats (Crossland et al. 1984; Schaffelke & Klumpp 1997; Ateweberhan et al. 2005a). During the hot season, algal turfs are more abundant in terms of cover (Ateweberhan et al. 2006a; Afeworki et al. 2011) but have lower height (standing crop) (Ateweberhan et al. 2006a). It is known that low turfs harbour less sediment and hence have high quality detritus (Purcell 2000; Purcell & Bellwood 2001; Wilson et al. 2001). Given this, the EAC in summer is expected to be of better quality and increased intake during this season sustains fast growth and increasing body condition.

The positive correlation between energy reserves and growth rate in *S. ferrugineus* is to be expected, since both are likely to occur during periods of food abundance (Jobling 1988; van Rooij et al. 1995b). Liver weight in this species shows similar temporal dynamics as body condition and peaks during the warm season (see also Chapter 7). In contrast, investment in gonad and reproductive behaviour in *S. ferrugineus* peaks during the cool period of the year between December and March (Chapter 7). This agrees well with the observation that in seasonal environments reproduction is relegated to the season where food availability is minimal (Fishelson et al. 1987; Montgomery & Galzin 1993; Caceres et al. 1994; Varpe et al. 2009). This may partly be due to a trade-off in time allocation between feeding and reproductive activities such as courtship (van Rooij et al. 1996a; Kolluru & Grether 2005) and partly due to a trade-off in energy allocation between reproduction and somatic growth (Reznick 1985; van Rooij et al. 1995b).

Parrotfishes spend over 90% of the day light hours foraging on a low nutrition diet (Bruggemann et al. 1994, Afeworki pers. obs.). Trade off in time between reproduction and feeding may therefore be expected. Spawning activity in these fish may last from 1 to 3 hours per day (van Rooij et al. 1996a, Afeworki pers. obs.), resulting in a substantial reduction of feeding time. In *S. ferrugineus* this leads to a 23% lower daily intake in reproducing TP compared to similar-sized males not engaged in reproductive activity (Afeworki et al. 2013). Recognizing the importance of this conflict, Robertson (1991b) suggested that this may have influenced the timing of reproduction in coral reef grazers. The tendency of coral reef grazers to spawn at dusk or dawn (Colin & Clavijo 1988; Colin & Bell 1991; van Rooij et al. 1996a; Craig 1998; Sancho et al. 2000b; Kuwamura et al. 2009) appears to be an adaptation to avoid spawning during the noon and early afternoon periods when both the nutritional quality of algae and the feeding rates of grazers are at their peak (Polunin & Klumpp 1989; Zoufal & Taborsky 1991; Bruggemann et al. 1994; Zemke-White et al. 2002).

Similarly, *S. ferrugineus* may avoid this conflict by lowering time spent in reproductive activity during times of the year when food is abundant. Energy stored during this period of enhanced feeding may subsequently be used for gamete production during the cool season. Fishelson et al. (1987) reports such mechanism in the surgeonfish *Acanthurus nigrofuscus*. These observations suggest that coral reef fishes in seasonal environments can behave like capital breeders (sensu Drent & Daan 1980) where resources stored at one point in time are used to fuel reproduction at another.

Feeding rate, growth and body energy reserves are positively correlated with irradiation, temperature and food availability. Since the different environmental factors have not been controlled for, it is difficult to evaluate their separate roles. Elevated temperature is known to reduce growth either by lowering feeding rates or by increasing metabolic costs (Jobling 1994; Koskela et al. 1997; Thyrel et al. 1999; Donelson et al. 2010). However, the negative effect of high temperature is partly offset when food supply is high (Munday et al. 2008). For *S. ferrugineus* the steep decline in growth rate from August onward when temperatures are still high (33°C – 34°C) but availability of algal turfs on the fore reef is on the decline (Fig. 5.2B), suggests that food limitation in combination with extreme high temperature may curb somatic growth.

5.4.2 Correspondence between availability of algal functional groups and growth of grazers

Temporally varying rates of growth and body condition in coral reef fishes have been reported from a variety of locations (Fishelson et al. 1987; Montgomery & Galzin 1993; van Rooij et al. 1995b; van Rooij et al. 1995a). However the extent of the variation reported here is extreme and is akin to that occurring in temperate systems. This reflects the highly seasonal nature of the southern Red Sea where monsoon driven changes in temperature are known to cause significant changes in biomass and composition of algae (Ateweberhan et al. 2005a; Ateweberhan et al. 2005b; Ateweberhan et al. 2006b). The monsoons are likewise responsible for seasonality in marine biological processes in the western Indian Ocean including algal growth, fish reproduction and recruitment (Fishelson et al. 1987; McClanahan 1988; Ormond & Banaimoon 1994; Abou-Aisha et al. 1995). The way in which this seasonality affects reef grazers however differs and appears to be related to their feeding habits. For example, in the northern Red Sea surgeonfishes have peak body conditions during the cool season, which is associated with the increased availability of green foliose macroalgae (Fishelson et al. 1987; Montgomery & Galzin 1993). Contrastingly, body condition in the rabbitfish *Siganus rivulatus* – a species that feeds on canopy forming brown seaweeds (Lundberg & Lipkin 1979; Lundberg & Golani 1995; Ateweberhan 2004) – at Egyptian reefs is highest during summer months (Hanna 1984) when these macroalgae are at their peak abundance. In *S. ferrugineus* peak growth and body condition occur in spring and summer when EAC are abundant. It appears therefore that different members of the grazer guild may face seasonality in life processes related to their respective feeding habits. This suggests that changes in benthic communities will affect the population dynamics of different functional groups of grazers differently leading to changes in community structure of the grazers. For example, events that lead to the dominance of macroalgae are more likely to augment population growth of macroalgivores (such as siganids) at the expense of scarids.

5.4.3 Sex change and growth spurt

Sexual size dimorphism (SSD) in sex changing species is a common phenomenon (Choat & Robertson 1975; Robertson & Warner 1978; Sadovy & Shapiro 1987) and is essentially linked with a polygynous reproductive mode where large size in males is crucial in monopolizing mating (Warner 1988b; Munday et al. 2006). The size structure of *S. ferrugineus* conforms to the "typical protogynous pattern" (Choat & Robertson 1975; Robertson & Warner 1978; Sadovy & Shapiro 1987) where the largest size classes are dominated by TP (Afeworki 2003). SSD in *S. ferrugineus* is further confirmed by the larger asymptotic length of TP (34.5 cm) compared to that of the IP (25.1 cm; Table 5.4).

It has long been recognized that the proximate cause of SSD is difference in the growth history of the two sexes (Badyaev 2002). Recent works on coral reef sex-changing species have identified two growth processes that lead to SSD. One involving faster growth (growth spurt) following sex change (Walker & McCormick 2004; Munday et al. 2009; Walker & McCormick 2009) and a second process in which the sex changing individuals are inherently faster growing (Francis & Barlow 1993; Adams & Williams 2001; Walker et al. 2007). That the individual growth variability of the IP ($v = 0.70$) is within the reported values for many fish species (Welsford & Lyle 2005) suggests that the IP in *S. ferrugineus* is not composed of subgroups with divergent growth characteristics. Furthermore, a parallel study on demography and sex change in *S. ferrugineus* using age based methods indicated that initial phase males have similar growth to initial phase females (Chapter 6). It appears that growth acceleration during and following sex change is the dominant process for the SSD in *S. ferrugineus*.

During sex change individuals lose in fitness because their reproductive output is zero (Hoffman et al. 1985; van Rooij et al. 1996a). By postponing reproduction, TIP presumably direct a larger portion of their energy for growth to attain larger size which will enable them to compete for spawning territories later (Hoffman et al. 1985). Following sex change, TP continue to grow fast or attain better body condition (van Rooij et al. 1995b; van Rooij et al. 1995a) suggesting that reproductive investment in TP continues to be low as long as TP are not large enough to occupy a spawning territory (van Rooij et al. 1996a).

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CHAPTER 6

SEX-SPECIFIC DIFFERENCES IN DEMOGRAPHY IN A SEQUENTIAL HERMAPHRODITE: IMPLICATIONS FOR SEX CHANGE MODELS

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Abstract Annual growth bands read from transverse sections of sagittae were used to study growth, longevity and mortality rate differences between males and females of the protogynous parrotfish *Scarus ferrugineus* in the southern Red Sea, Eritrea. Three life phase categories were recognized, initial phase (IP) females, IP males, and terminal phase males (TPs). Growth rates of IP males were not different from those of IP females. An IP male had longer life span than TPs, suggesting that not all IP males change colour to become TP male. IP females and TPs differed significantly in all tested demographic parameters. TPs grow faster (von Bertalanffy growth constant of 0.3 vs. 0.23) and reach larger asymptotic sizes (34 cm vs. 24 cm) than IP females. The mean length of TPs at ages 3, 5, 7 years is 24-37% higher than that of an IP female. The natural mortality rate of TPs was higher than that of IP females. This could possibly be related to the extreme temperature of the habitat, the high energetic loss in territory defence and or increased predation risk during spawning. Longer life spans of IPs (10 years) than TPs (8 years) indicates that some IPs remain female for life. The existence of gonochoristic females (none sex changers) appears to be due to the higher male mortality that sets an upper threshold age of sex change beyond which expected reproductive output as sex changed individual will be low.

To be submitted

6.1 Introduction

Parrotfishes (family Labridae) are common coral reef fishes with a complex life history that involves sex change and diverse mating strategies ranging from group spawning to haremic and lek systems (Choat & Robertson 1975; Robertson & Warner 1978; van Rooij et al. 1996a). Labrids in general are sequential hermaphrodites typically starting life as females (initial phase, IP) changing later to males (terminal phase, TP) (Robertson & Choat 1974; De Mitcheson & Liu 2008). The two life phases generally show distinct colour and size dimorphism, where the larger sized males are brightly coloured and the females are drab. In some species the initial phase is entirely composed of females and all the TP are therefore derived from an initial female phase - a system called monandry (Robertson & Warner 1978). The majority of labrids are diandric, however, where some percentage of the IP fish (IPs) are males, in which case TP individuals (TPs) may either be derived from IP females (and are called secondary males) or from IP males (called primary males) (Robertson & Choat 1974).

The size advantage hypothesis (SAH) has been proposed to explain patterns in sex change in sequential hermaphrodites (Ghiselin 1969; Charnov 1982; Warner 1988b). The SAH states that if reproductive output in one sex increases with size/age at a higher rate than the opposite sex, then an individual maximizes its lifetime reproductive output if it starts life as the sex with the slow increase rate then switch to the other sex at an older age. For example if reproductive output in males increases with size/age more steeply than that of females, protogyny (sex change from female to male) is predicted. In its original form the SAH treated reproductive output (fecundity) in relation to size/age alone, but later developments have noted that the reproductive output can vary due to demographic differences (growth, mortality) (Charnov 1982; Iwasa 1991). Theory shows that if the sexes differ in growth rate, individuals maximize their lifetime reproductive output if they start life as the fast growing sex and later switch to the slower growing one. Differential mortality between the sexes favours individuals that change sex from the low mortality sex to the high mortality sex. Besides size/age specific fertility and demography, the reproductive output of males and females can also be greatly influenced by the mating system. For example in haremic and lekking systems where mating is monopolized and high reproductive output is accrued by large males, protogyny is favoured (Robertson & Choat 1974; Choat & Robertson 1975; Warner 1988b; Munday et al. 2006).

Given the various factors that affect the reproductive output of an individual male or female, the expected lifetime reproductive output (reproductive value) will be a function of its age/size specific fecundity, its growth potential, probability of survival and the probability of acquiring a territory or harem (Charnov 1982; Warner 1988a; Warner 1988b). Since the demography and mating strategies of populations vary in space and time (Warner & Hoffman 1980a; Shapiro 1991; Gust et al. 2002), sex change is expected to be highly flexible (Cowen 1990; Munday et al. 2006). Likewise, if two or more of the different factors act in opposite directions, this may lead to the loss of hermaphroditism (Charnov 1986).

An increasing amount of evidence, ranging from condition-dependent bi-directional sex change (Nakashima et al. 1995; Munday et al. 1998; Kuwamura et al. 2002) and highly variable size/age at sex change within species (Cowen 1990; Collin 2006; Molloy et al. 2011), to condition-dependent deferral of sex change (none-sex-changing females) (Munoz & Warner 2003a; Munoz & Warner 2004), support the notion that sex change indeed is flexible. The proximate cues used to initiate sex change are derived from the social and demographic conditions; including population density (Lntnesky 1994; Zhang & Lin 2007; Caselle et al. 2011), sex ratio (Shapiro & Lubbock 1980), rank in the social hierarchy (Robertson 1972; Shapiro 1980; Shapiro 1981; Warner & Swearer 1991), and age structure (Charnov 1982).

It is clear from the above that studying demography is, key to understanding patterns of sex change in sequential hermaphrodites. Age-based demographic studies of coral reef protogynous species are, however, not common (Choat & Robertson 2002) and studies on sex change are typically based on size (Choat & Axe 1996; Allsop & West 2003). Despite its popularity, length-based demography is unreliable for coral reef fishes due to the rapid initial growth of reef fishes ("square" growth curve), a phenomenon that leads to the decoupling of length and age (Choat & Robertson 2002). In many reef fish taxa, including labrids, juveniles converge into adult sizes in the first few years of life (Choat & Axe 1996; Choat et al. 1996; Zekeria et al. 2006), resulting in aggregation of nearly all age classes (spanning the entire life span of the species) within a narrow adult size interval. Age-based analyses provide an entirely different view of the demography (Choat et al. 1996). For example, the protogynous size structure (large sizes dominated by TPs) and sexual size dimorphism of labrids are not due to TPs being older, as previously assumed, but are the result of growth rate differences between the sexes, either due to growth spurt following sex change or due to sex changing individuals being inherently faster growing (Choat et al. 1996; Adams & Williams 2001; Munday et al. 2004; Walker & McCormick 2004; McCormick et al. 2010). Therefore, using length as a measure of the timing of sex change is likely to give an erroneous impression of a narrow window of age-at-sex change. It is therefore important to study sex change dynamics in reef fishes using age rather than length.

Age-based studies of labrids also led to the discovery of none-sex-changing females, individuals that are as old as or even older than males (Choat et al. 1996; Munday et al. 2004; Choat et al. 2006). The existence of old and large none-sex-changing females in haremic species such as *Sparisoma radians* (Munoz & Warner 2003b; Munoz & Warner 2004; Manabe et al. 2008), clearly poses a challenge to the traditional SAH (Munoz & Warner 2003b; Clifton & Rogers 2008). Munoz and Warner (2003b), suggest that in circumstances where the fecundity of the dominant (largest) female in a harem is higher than the aggregate of the subordinate females in her social group (size fecundity skew), this female does better if she defers sex change. Alternatively a large/older female may defer sex change if her expected reproductive value as a sex changed male is low due to high mortality in males (Clifton & Rogers 2008). Why large females fail to change sex is likely to be due to a combination of social factors, demography and size fecundity skew (Zhang & Lin 2007; Warner & Munoz 2008). Age-based methods, by revealing differences in growth, mortality, and longevity between males and females, have the potential to answer why certain females do not change sex.

Here we report the existence of older none-sex changing females in a *Scarus ferrugineus* population and show that this is due to sex-specific differences in mortality rate. This work was inspired by a previous study that found significant differences in longevity between males and females of *S. ferrugineus* in two southern Red Sea populations (separated by 600 km) (Afeworki 2003). Here we expand on this by extensive sampling of male and female *S. ferrugineus* from one population and studying its size structure, sex ratio, age structure, growth, longevity and mortality rate.

6.2 Materials and Methods

6.2.1 Study site and study species

Fish collection and underwater visual census were conducted on the windward fringing reef of Sheik Said Island, Massawa, Eritrea (15°35′N; 39°29′E). Despite its inshore location and proximity to the city of Massawa, the reef has high coral cover (30 – 50%) (Zekeria & Videler 2000; Afeworki et al. 2011) and supports a diverse and abundant grazer guild (Afeworki et al. 2013). There is a low intensity, canoe based, fishery around Massawa, but parrotfishes or other reef grazers are not targeted (Tsehaye et al. 2007). The area experiences two distinct monsoon-associated seasons, the cool season from December to March and a hot season from May to October. Benthic algal communities, corals and fish are strongly affected by this seasonal change in environmental conditions (Ateweberhan et al. 2006a).

The study species *Scarus ferrugineus* is endemic to the Red Sea and Arabian Sea (Randall 1983). In the southern Red Sea it is the dominant grazer, representing 34% of the total herbivorous fish biomass (Afeworki et al. 2013). *S. ferrugineus* like most parrotfishes is a diandric protogynous hermaphrodite with two life phases: the initial drab and mostly female IP and the terminal and colourful male TP (Randall & Ormond 1978; Abdel-Aziz et al. 2012).

6.2.2 Sex determination and otolith samples

Five IPs and five TPs were collected every month by spearing between 2006 and 2007, with additional samples (31 individuals) collected in 2008. To cover the whole size range (0 – 36 cm), additional samples were collected using small-meshed barrier nets particularly targeting the smaller size classes. In the lab, fork length (FL), body depth, body mass and gutted mass were recorded, otoliths (the left and right sagittae) were extracted and the life phase of each individual noted. Visual examination of the reproductive organs was used to distinguish between males and females in the IP. In this study we identified four sexual categories: Initial phase females (IP females), Initial phase males (IP males), and terminal phase males (TPs) and individuals in the process of colour/sex change – identified due to their intermediate colouration - were recorded as transitional (TIPs). We did not differentiate between primary and secondary TPs. Demographic analysis of IP females and IP males was done separately. To validate the periodicity of annulus formation both marginal increment analysis and oxytetracycline tagging of otoliths were used. Fish (30 individuals) were captured using barrier nets and injected size dependent doses of oxytetracycline in the abdominal cavity (McFarlane & Beamish 1987). Furthermore, alphanumeric tags (VI alpha tags: Northwest Marine Technology, Inc) were implanted between anal fin rays to identify the oxytetracycline injected fish.

6.2.3 Otolith processing and interpretation

Left and right sagittae were cleaned using household bleach, rinsed with fresh water and air dried for further analysis. Either the left or the right sagitta was randomly selected for sectioning. After embedding the sagittae in transparent polyester resin (Sody 33 ESCIL, Chassieu, France), a thin transverse section containing the primordium was cut using a low speed diamond saw (Isomet, Beuhler, Illinois, USA). Sections were mounted on glass slides using thermoplastic glue (Crystallbond) and ground on polishing paper of grain sizes 800 μm followed by 1200 μm on either side until the primordium was visible from both sides. Finally the section was mounted with the anterior side up and was further fine polished serially using aluminium powder of 3, 0.1 and 0.03 μm grain size. Previous studies of otolith structures of fish in the southern Red Sea indicated that the seasonal nature of the environment promotes annual band formation in reef fishes (Zekeria et al. 2006). These alternate opaque and translucent bands were read by reflected white light (200 x magnification) along a line extending from the primordium to the ventral rim of the sulcus. Replicate readings were conducted three times by the same observer (Y.A.) at ≥2 week intervals. Sections whose annuli counts were the same on ≥2 readings were taken as the final age; sections with different readings (even by one annulus) on each occasion were discarded from further analysis.

6.2.4 Growth modelling

The standard von Bertalanffy growth function (VBGF) (Equation 5.1) was fitted to sex specific age-length data to describe the overall growth pattern. The three parameters of this model are the theoretical mean asymptotic length (L_∞), the growth rate coefficient (k) and the theoretical mean length at age zero (t_0).

$$L = L_\infty \left(1 - \mathrm{e}^{k(T - t_0)}\right). \tag{6.1}$$

The standard VBGF parameters have statistical properties (e.g. strong co-correlation, nonlinearity) that render them difficult to use for comparisons between populations (Francis 1988b; Cerrato 1990; Cerrato 1991). Thus for the comparison of growth rate between males and females we used a three-parameter reparametrized version of the VBGF (rVBGF) (Equation 5.2) (Francis 1988b). The new parameters are l_τ, l_υ and l_ω and refer to mean lengths at ages τ, υ, and ω (where $\omega = {}^{(\tau + \upsilon)}/_{2}$; ages in years). These parameters have a direct biological meaning since they represent the mean lengths at selected ages drawn from the data. Moreover they have better statistical properties due to their lower correlation and tendency to behave like linear equations (Francis 1988b). We selected the ages where the TP and IP overlap namely $\tau = 3$, $\omega = 5$, $\upsilon = 7$.

$$L_T = L_\tau + \frac{(l_\upsilon - l_\tau)\left(1 - r^{2(T-\tau)/(\upsilon-\tau)}\right)}{1 - r^2}, \tag{6.2}$$

where $r = \frac{l_\upsilon - l_\omega}{l_\omega - l_\tau}$.

Model parameters were estimated by fitting the length-at-age data using a nonlinear regression procedure by minimizing the negative log likelihood function (Equation 5.3) in SPSS version 16.

$$-\lambda = -\sum_i \ln\left(\frac{1}{\sqrt{2\pi\sigma}}\exp^{-\frac{(L_i-\mu_i)^2}{2\sigma^2}}\right). \tag{6.3}$$

Data sets for the IP and TP were bootstrapped (5000 times with replacement) and parameters for each bootstrap sample estimated. From the distribution of the bootstrapped estimates, a 95% confidence interval was estimated by taking the 2.5 and 97.5 percentile points as the lower and upper limits respectively. Significance of difference in growth between the sexes was assessed visually by examining the degree of overlap in the confidence regions of the growth parameters.

6.2.5 Size structure, age structure and mortality

Underwater visual censuses (UVC) were conducted at least twice a year between 2006 and 2008 to assess the density and size structure of the study population. Counts were undertaken on six replicate 30*5 m transects in each of four reef zones (reef flat, reef crest, shallow fore reef and deep fore reef) both at high and low tide. IPs and TPs were classified into 5 cm size classes and their abundance recorded. Size structure data from UVC between different seasons within the year and between years was compared using chi-square tests. To test if our catch data was representative of the size structure of our study population we compared size structure of our catch data with that of the UVC.

Sex-specific mortality rate was estimated from the age frequency distribution using the standard catch-curve analysis by regressing the log of frequency on age. Ages to the left of the modal age were left out of the analysis. Since fishing mortality is virtually absent, this mortality estimate is considered to represent the natural mortality in the study population. Sex change translates into loss of individuals from IP to inflate TP abundance, which will influence mortality estimates. We did not account for this effect, as a result, the natural mortality of IPs will be slightly overestimated and that of TPs will be underestimated.

The proportion of IP males in the *S. ferrugineus* population was estimated from the present catch data. Since the number of IP males and TIPs captured in this study was small, we added data of *S. ferrugineus* caught for tagging purposes at the same site between 2006 and 2008 to obtain size distributions for TIPs and IP males. In this study, IP males were identified by gently applying pressure on the abdomen to release gametes or semen and those individuals that secreted a milky substance were categorized as males, while TIPs were identified by the colour changes that accompany sex change. Size at sex change (FL_{50}) and age at sex change (A_{50}) are defined as the size/age at which 50% of the individuals are TPs. Binomial logistic regression was used to determine FL_{50} and A_{50}.

6.2.6 Longevity

Longevity of IPs and TPs was estimated in two ways. The first estimate is the maximum recorded age for each life phase. However, this may overestimate longevity in cases where sample size is small or where there are outliers in the data (Gust et al. 2002). A more reasonable albeit conservative estimate is mean maximum age (mean T_{max}), given as the average

Table 6.1 Sample size and sex composition of the catch used to study the demography of the *Scarus ferrugineus* population at Sheikh Said Island, southern Red Sea, Eritrea.

Life phase	Sample size (n)	Size range FL (cm)	Age range (years)
IP females	127	8.8 – 27.5	1 – 10
IP males	7	15.7 – 24.0	2 – 9
TIP	3	21.4 – 25.2	2 – 7
TP	95	18.5 – 36.5	2 – 8

age of the oldest 10 or 20% of the catch (Gust et al. 2002). Here, mean T_{max} was taken as the average age of the oldest 10%.

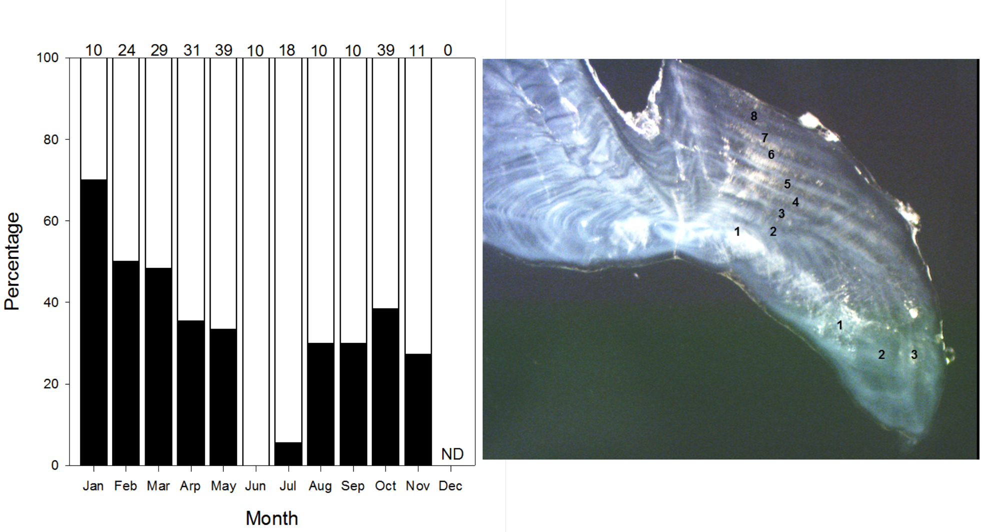

Fig. 6.1 *Scarus ferrugineus.* (Left) Annual trend in the prevalence of opaque (black) and translucent (white) bands on the margins of transverse otolith sections. Numbers above are sample sizes for each month. (Right) Annual growth bands in a transverse section of a sagittae from an 8 year old, 23.3 cm (fork length) initial phase individual.

6.3 Results

A total of 243 fish were collected, 11 (4.5%) otoliths were damaged during processing or were unreadable (see Table 6.1 for sample details). *S. ferrugineus* otolith sections generally had readable opaque and translucent bands (Fig. 6.1). Two of the oxytetracycline injected fish were recaptured after one year at liberty, but only one showed a clear fluorescent mark in the otolith. Both the otolith tagging and marginal increment analysis indicated that growth bands

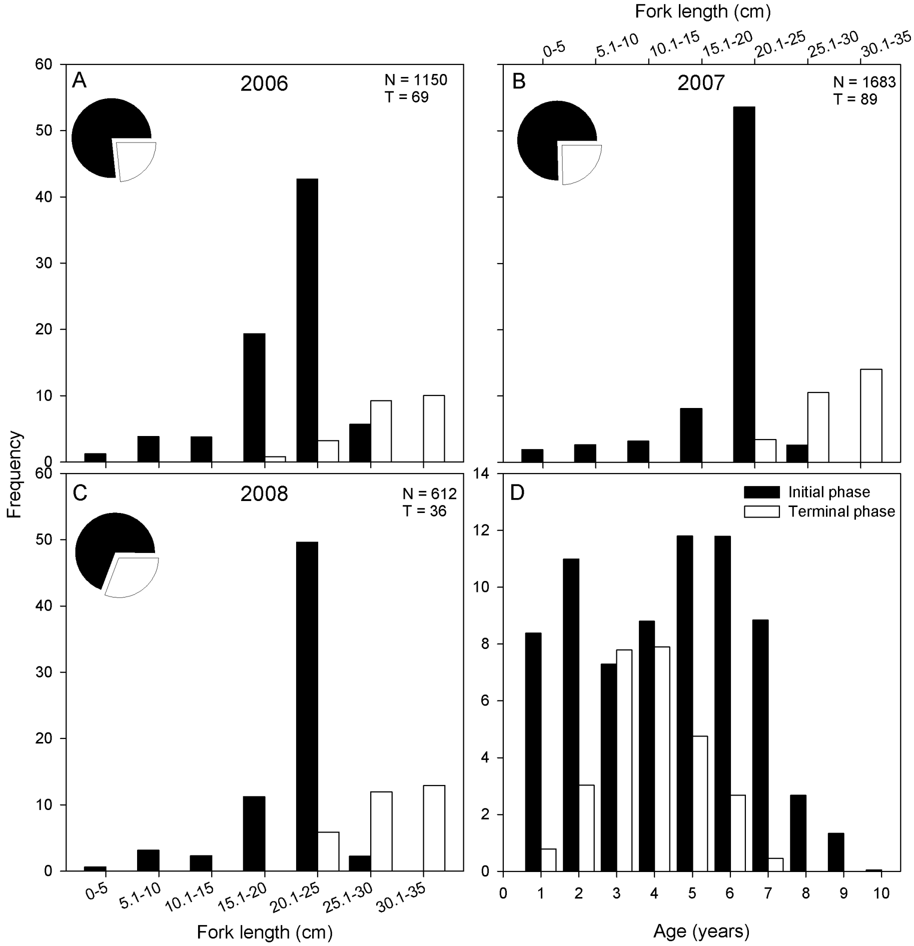

Fig. 6.2 *Scarus ferrugineus*: Sex-specific size and age structure at the fringing reef Sheikh Said Island, southern Red Sea, Eritrea. (A),(B),(C) Size structure estimated from underwater visual census during three consecutive years. N: total number of individuals counted; T: number of transects surveyed. Pie-charts indicate the proportion of IPs and TPs in the population. (D) Age structure.

are formed once a year (Fig. 6.1) with the deposition of opaque bands occurring during the cool season. Since this season is the time of slow growth (Chapter 5) the opaque band in *S. ferrugineus* is associated with reduced growth.

6.3.1 Size and age structure

Size structure ($\chi^2 = 5.295$, $df = 8$, $P = 0.726$) and sex ratio ($\chi^2 = 1.645$, $df = 2$, $P = 0.439$) of the study population remained stable between 2006 and 2008 (Figs. 6.2A-C). The mean proportion of TPs in the population was 27±2.16% (mean±SE). The two life phases overlap in size from 18 cm to 27.5 cm. The observed size range of IP males was 15 – 24 cm while TIPs ranged from 19 – 26 cm (Fig. 6.3C). FL_{50} and A_{50} were 25.89±1.5 cm and 2.89±0.74 years.

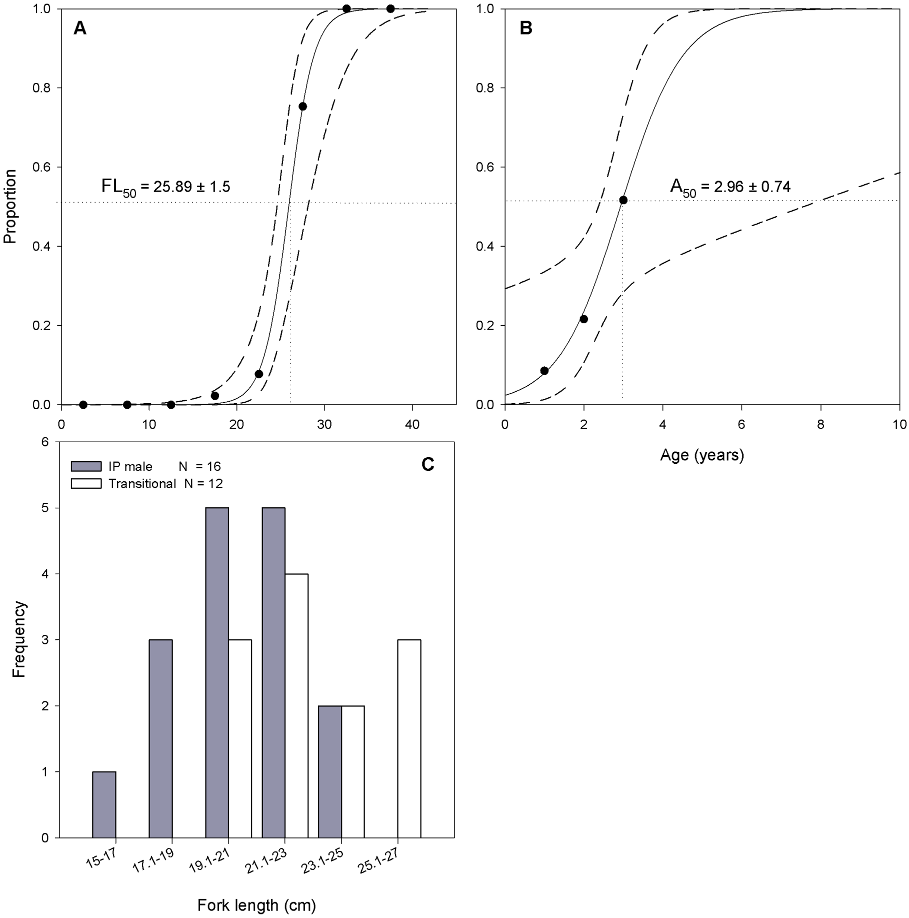

Fig. 6.3 *Scarus ferrugineus*: Logistic curves showing the length (A) and age (B) at sex change. (C) Size frequency distribution of initial phase males and transitional individuals, Sheik Said Island, southern Red Sea, Eritrea.

Size structure of our catch differed significantly from that recorded with UVC ($\chi^2 = 99.989$, $df = 7$, $P = 0.000$). Separate tests for IPs ($\chi^2 = 8.255$, $df = 4$, $P = 0.083$) and TPs ($\chi^2 = 10.337$, df

= 2, $P = 0.006$) indicated that the source of the difference was increased sampling of the 30 – 35 cm size class of TPs. Given these observations, the mean of the three years of UVC estimates was taken as the final size structure of the population. IP and TP size frequency distributions from the UVC were converted into age frequency distribution by multiplying this by the proportion of ages recorded for each size class from the catch. The age frequency distributions of IPs and TPs (Fig. 6.2D) are unlike the size frequency distributions for these life phases. IPs dominate the smaller and TPs the larger size classes. The age frequency distribution shows a contrasting pattern of older individuals being dominated by females.

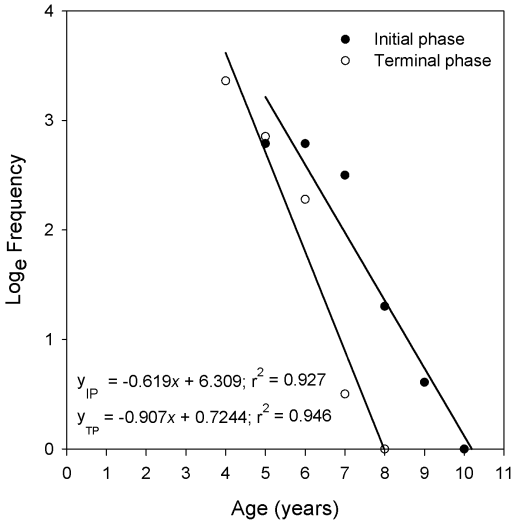

Fig. 6.4 *Scarus ferrugineus.* Age based catch-curves of initial phase and terminal phase *Scarus ferrugineus* from Sheik Said Island, southern Red Sea, Eritrea. Equations of the lines and r^2 are given.

Natural mortality rate was significantly higher in TPs compared to IPs (ANCOVA: $F_{1,11} = 17.385$, $P = 0.003$; Fig. 6.4). Moreover both measures of longevity indicate that IPs live significantly longer than TPs (t-test: T_{max}: $t_{2,23} = 3.785$, $P = 0.001$) (Table 6.2).

6.3.2 Growth

The growth parameters obtained for the *S. ferrugineus* population are detailed in Table 6.2. Growth rate of IP females was highly asymptotic resembling the “square” growth curve of many reef fishes while TPs seem to grow continuously (Fig. 6.5A). TPs achieved significantly larger mean sizes for a given age compared to IPs (Figs. 6.5A,B & 6.6).

The proportion of IP males in our study population was 5% (Table 6.1). Due to the small sample size of IP males, it was not possible to fit an independent VBGF for this category. Therefore we compared the mean lengths at ages 2 and 5 years (ages where we had at least 3 IP males sampled). Mean lengths at these ages did not differ between IP females and IP males (ANOVA: 2 years: $F_{1,17} = 2.34$, $P = 0.15$; 5 years: $F_{1,21} = 2.78$, $P = 0.11$; Fig. 6.7) suggesting similar growth rates between IP females and IP males. However, IP males tended to have smaller sizes at these ages than IP females, indicating that they may grow somewhat slower.

6.4 Discussion

6.4.1 Growth and sexual size dimorphism

S. ferrugineus is a diandric protogynous hermaphrodite a trait that is common among the parrotfishes (Abdel-Aziz et al. 2012, Chapter 7). Large TPs adopt a haremic or lek based spawning strategy while IP males use a group spawning or sneaker strategy (Chapter 7). Growth in IP males is somewhat slower (but not significantly different) from that of IP females, suggesting that reproductive investment in IP males is equivalent to or even higher than that of IP females. Active participation in spawning and large testis size in IP males is likely to affect IP male growth rates. A recorded age of 9 years for an IP male suggests that these may have longer life spans than TPs, indicating that some individuals retain this reproductive strategy for life. These observations suggest that being an IP male is not a strategy to defer current reproduction to grow fast and reach territorial status (through colour change), but rather an alternative mating tactic of a subset of the male population.

S. ferrugineus demonstrates clear sexual size dimorphism (SSD). Large size classes are dominated by TPs and at any given age TPs attain larger size than IPs. The observations that growth rate in IP males is not significantly different from IP females (this study) and that TIPs grow faster than IPs and TPs (Chapter 5) strongly suggest that a growth spurt following sex change is the cause of this SSD. Sex-specific differences in growth rates (Choat et al. 1996; Choat et al. 2006; McCormick et al. 2010) and the fast initial growth (Choat & Robertson 2002; Zekeria et al. 2006) make length a poor indicator of age in reef fishes. For example, the square growth curve of IP females results in the aggregation of almost all age classes (2 –

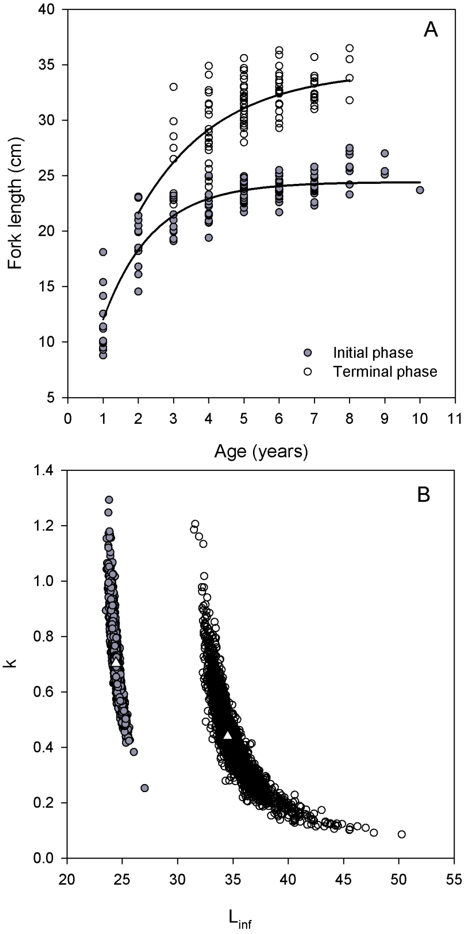

Fig. 6.5 *Scarus ferrugineus*: (A) Standard von Bertalanffy growth function (VBGF) fitted to length-at-age data of initial phase and terminal phase fish sampled from Sheikh Said Island, southern Red Sea, Eritrea. (B) Distribution of 5000 bootstrap estimates of the VBGF parameters K (the growth coefficient) and L_∞ (mean asymptotic length). Parameter estimates of the original data are shown as open triangles.

8 years) in the 20 – 25 cm size range (this study). In *S. ferrugineus*, transitional individuals occurred over an age interval of 5 years, amounting to approximately half the life span of the study population. In contrast the window of sizes-at-sex change (19 – 25 cm) is much narrower, covering only 17% of the adult size range. A wider overlap between the sexes in age (usually complete overlap) than in length is a common feature of protogynous fishes (Gust 2004; Pears et al. 2006; Cossington et al. 2010). This appears to be a consequence of the "square growth" that is characteristic of reef fishes.

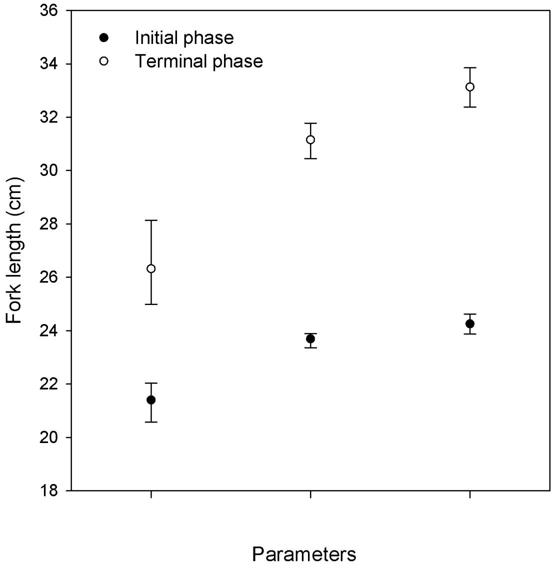

Fig. 6.6 *Scarus ferrugineus*. Mean lengths and 95% confidence intervals generated from 5000 bootstrap estimates using the percentile method. Mean lengths at the ages (3 =L_3; 5 = L_5 and 7 = L_7) from the reparametrized von Bertalanffy growth function.

6.4.2 Sex-specific demography, growth, and sexual dimorphism

TPs in our population suffered a higher mortality and as a result had shorter life spans compared to IP females and IP males. Possible factors that contributed to the high mortality are a) the extremely high summer temperature; b) high energetic cost associated with territorial activity, and c) increased predation risk. Elevated temperature is generally associated with increased mortality in ectotherms such as fish (Pauly 1980; Robertson et al. 2005; Trip et al. 2008; Bevacqua et al. 2011). Summer sea surface temperatures (SST) at our study site (32 – 34°C) are higher than in most coral reef habitats (Ateweberhan et al. 2006a; Zekeria et al. 2006). Moreover, rapid rise in SST in the mid 1990s in the Red Sea has accentuated the already extreme nature of the habitat (Raitsos et al. 2011, Box 1.3). Such temperatures are generally considered to be critical for many coral reef fishes (Mora & Ospina 2001; Munday et al. 2008; Nilsson et al. 2009). Higher mortality in the larger bodied TPs is to be expected since the temperature associated mortality is more pronounced for large individuals (Hernandez et al. 2002; Peck et

Fig. 6.7 *Scarus ferrugineus*: Mean length (±SE) at ages 2 and 5 years of initial phase females and initial phase males.

al. 2009; Morita et al. 2010). Indeed, Afeworki et al. (2013) recorded reduced feeding rates in large TPs during summer compared to the smaller sized IPs suggesting that large TPs in our study site may live close to their upper thermal limit. Within the southern Red Sea parrotfish populations from the hottest sector i.e. Massawa (the current study site) have lower asymptotic sizes and lower life spans compared to the slightly cooler Assab area (Afeworki 2003). The latter two observations suggest that temperature may be an important cause of mortality difference between the sexes.

Large TPs expend considerable energy associated with territory defence (Grantner & Taborsky 1998; Buchanan et al. 2001; Castro et al. 2006). Furthermore, large TPs in our *S. ferrugineus* population lose 23% of the daily food intake due to their territorial activity (Afeworki et al. in review). Reports have shown that such losses may result in low growth rates and low body condition in territorial compared to none territorial individuals (van Rooij et al. 1995b; van Rooij et al. 1995a). Large TPs are therefore likely to experience increased mortality rates due lowered body condition (Dutil & Lambert 2000). Moreover poor body condition and high temperature tend to act synergistically whereby fish in poor condition at extreme temperatures have low survival rates (Robinson et al. 2008).

Finally, large males may suffer high mortality due to sex-specific predation. Studies have shown that predation is an important determinant of demography in labrids (Gust et al. 2002; DeMartini et al. 2005) and that spawning episodes are the most vulnerable moments (Sancho 2000; Sancho et al. 2000a). As territorial TPs typically engage in repeated courtship and spawning rushes (the most vulnerable moment) with different IPs (Moyer 1986; Clifton & Robertson 1993; Sancho 2000), spawning associated predation is expected to be higher for TPs

Table 6.2 Summary of the demography of initial phase and terminal phase *Scarus ferrugineus* from Sheikh Said Island, southern Red Sea, Eritrea. VBGF: standard von Bertalanffy growth parameters; K the growth rate coefficient, L_∞ the mean asymptotic length, and to the theoretical length at age zero. rVBGF: growth parameters of the reparametrized VBGF L_3, L_5 and L_7 mean lengths at ages 3, 5 and 7 years respectively. Values in parenthesis are the upper and lower boundaries of the 95% confidence interval.

Model/Parameter		Life phase	
		IP	TP
VBGF	L_∞ (cm)	24.43 (23.77 to 25.09)	34.52 (28.71 to 40.34)
	k (yr^{-1})	0.704(0.465 to 0.952)	0.44 (0.136 to 0.751)
	t_0 (yr)	0.035 (-0.427 to 0.498)	-0.239 (-3.217 to 2.739)
rVBGF	L_3 (cm)	21.40 (20.58 to 22.21)	26.32 (24.98 to 28.13)
	L_5 (cm)	23.69 (23.42 to 23.96)	31.15 (30.45 to 31.78)
	L_7 (cm)	24.25 (23.68 to 24.66)	33.13 (32.40 to 33.85)
Mortality rate (Z±SE)		0.619±0.09	0.907±0.13
Survival rate (S)		53.85	40.37
T_{max} (yr±SE)		8.42 ±0.43	7.2 ±0.23
Max age (yr)		10	8

that for IPs. Indeed Clifton & Robertson (1993) report higher predation mortality for males than females in the Caribbean parrotfish *Sparisoma radians*. Similarly van Rooij & Videler (1997) recorded higher disappearance rate (supposed mortality) in territorial males of *Sparisoma viride*. In our study site, the blue fin (*Caranx melampygus*) and the giant trevallies (*C. ignobilis*) are potential predators of spawning fish. We have recorded several failed attacks on spawning pair of *S. ferrugineus* by giant trevallies. Following such attacks the entire lek is abandoned for a brief moment until the predator disappears. Although we did not witness a successful attack, the presence of such predators at the study site suggests that they may be potential sources of mortality for large TPs.

6.4.3 Females for life

An interesting aspect of the truncated TP age structure – i.e. TPs missing from older age classes - is the presence of older none-sex-changing females. These are analogous to the none-sex-changing females in *Sparisoma radians* (Munoz & Warner 2004). Large females can defer sex change if their expected reproductive output as TP is lower than when remaining IP female. This can happen in cases where there is high size fecundity skew within harems (Munoz & Warner 2003b; Munoz & Warner 2004) or if males suffer higher mortality than females (Clifton & Rogers 2008). Munoz & Warner (2003b; 2004) showed that a dominant female in a harem fares better by staying female than by changing sex if the cumulative fecundity of its subordinates is smaller than her own fecundity. Size fecundity skew is unlikely to lead to similar circumstances in lek-based mating systems, such as that of *S. ferrugineus*, where the breeding group is larger and more open. Males in leks have an enormous potential for breeding success which is very unlikely to be topped by the fecundity of a single female. In leks daily spawning rates of 20 to 100 have been recorded (Warner & Hoffman 1980b; Hoffman et al. 1985) and in *S. ferrugineus* 16 spawning per morning were witnessed (Chapter 7). The contrast in spawning success of TPs between harem and open spawning is exemplified in a Caribbean population of *S. viride*, where van Rooij et al (1996a) observed TPs within harems to spawn at much lower rate compared to large TPs that spawned in leks.

In *S. ferrugineus* mortality difference between the sexes explains why some females do not change sex. A model of the expected reproductive success of IPs and TPs shows that the high male mortality in *S. ferrugineus* by discounting the expected reproductive success (ERS) of males sets an upper threshold age. Beyond the threshold age, the ERS for a sex-changed individual is lower than if the individual remains a female (see Box 6.1 for details). Individuals that cross the threshold age without meeting the right social and demographic cues to change sex will function as females for life.

High mortality in males is associated with the truncated TP age structure (Paddack et al. 2009, this study). Truncated TP age structure can therefore be used as a direct indicator of higher male mortality. A review of published age-based studies in sex changing fishes reveals that many species fit this pattern, including groupers (Pears et al. 2006; Moore et al. 2007) and labrids (Choat et al. 1996; Choat & Robertson 2002; Gust 2004; Choat et al. 2006; Armagan 2010; Trip et al. 2011). This strongly suggests that higher male mortality may be a common characteristic of many sex changing coral reef fishes. The presence of large/old gonochoristic females in these species appears to be a direct result of this mortality difference. Likewise, exploited protogynous populations will be expected to have old none-sex-changing females since fishing selectively removes the larger individuals (mostly males) (Hawkins & Roberts 2004a; Molloy et al. 2007).

Box 6.1 Threshold age of sex change

Introduction

Sequential hermaphroditism is common among coral reef fishes (De Mitcheson & Liu 2008). According to Ghiselin's (1969) size advantage hypothesis (SAH), sequential hermaphroditism should occur when small/young individuals reproduce efficiently as one sex (e.g. female) and older individuals do better as the other sex (e.g. male). The SAH has been successful in explaining both intraspecific and interspecific sex-change patterns (Warner 1988b). In sex changing species, such as *S. ferrugineus* (Chapter 7), the SAH could explain at what age or size sex change should occur (Warner 1988a; Warner 1988b). Predictions by the SAH are easier to test when reproductive success is expressed as expected reproductive success (ERS) (Warner 1988b; Munoz & Warner 2003b; Warner & Munoz 2008). The *ERS* of an individual is the cumulative number of eggs a female expects to produce or a male expects to fertilize (Warner & Munoz 2008). The *ERS* will be influenced by mortality, growth, the probability of TPs of acquiring a territory and, finally, by sperm competition (Munday et al. 2006; Clifton & Rogers 2008; Warner & Munoz 2008). In protogynous species, individuals should change from female to male if the *ERS* as a sex-changed individual is higher than when it had stayed female.

Munoz and Warner (2003b) developed a new version of SAH that includes size-fecundity skew and sperm competition to help explain the phenomenon of large none-sex-changing females in haremic species. In *Sparisoma radians*, when a male is removed, a subordinate female could change sex, contrary to the predictions of SAH. If there is large-size fecundity skew and paternity loss due to sperm competition, a large female may produce more eggs than she would be able to fertilize as a haremic male. In such cases, the largest female is not expected to change sex as demonstrated by empirical results (Munoz & Warner 2004). While making an important contribution in sex-change theory by incorporating the effects of size-fecundity skew and sperm competition (Warner & Munoz 2008), this new model does not incorporate the influence of demographic parameters on sex-change (Munoz & Warner 2003b; Clifton & Rogers 2008).

Clifton and Rogers (2008) proposed a sex-change model that incorporates sex specific demographic differences as well as sperm competition. Here we modify this model to fit the social and mating system of our study population of *S. ferrugineus*. Model parameters are from the population of *S. ferrugineus* that we studied at Sheikh Said Island (Chapters 6, 7 & 8). These include demographic parameters, mating tactics, reproductive success of males, rates of streaking, fecundity etc. Using this model we attempt to understand why some females do not change sex in *S. ferrugineus*.

The model

S. ferrugineus at our study site spawn daily (see Chapters 7 and 8). Territorial terminal phase males (TTPs) visit their temporary spawning territories daily and engage in spawning. It remains uncertain whether females have similar spawning rates. In this model both males and females of *S. ferrugineus* are assumed to spawn daily. The *ERS* of an IP female of age *X* is given by:

$$ERS_{IP} = \sum_{X}^{X_{max}} (1 - \mu_{IP})^X \cdot F, \tag{6.4}$$

where X is the age in days, X_{max} is the maximum age, and μ_{IP} is the daily mortality rate. The age specific fecundity (F) is estimated from a best fit regression of gonad weight and age ($F = \exp\{a + {}^{b}/_{X}\}$, see Chapter 7 for details) with the parameters $a = 1.84$ and $b = -3.41$.

For an individual that changes sex at age *X*, the *ERS* will be a sum of the *ERS* when the individual functions as a smaller non-territorial TP plus the *ERS* as a TTP. As a small non-territorial TP, the individual only engages in streaking and group spawning while as a TTP the individual engages in pair-spawning. Although TTPs are known to streak into pair-spawning of neighbouring TTPs, this is rare (see Chapter 7) and we do not include this in our model. Our field records show that the minimum size for TTPs to acquire a territory is approximately 30 cm. The maximum size of an IP in the study site is approximately 25 cm. Thus a sex-changed individual will have to grow from ~25 to ~30 cm to acquire a territory. From the von Bertalanffy growth model of *S. ferrugineus* (Chapter 6), this size increase is expected to occur within one year. Given this, we assume that a sex changed individual will function as a non-territorial TP during one year. The *ERS* of a sex changed individual will therefore be given by:

$$ERS_{TP} = ERS_{sTP} + ERS_{TTP}, \tag{6.5}$$

where the ERS_{sTP} and ERS_{TTP} are *ERS* during the none-territorial and territorial phase of a TP respectively.

$$ERS_{sTP} = N_{IP} \cdot \bar{F} \cdot P \cdot Z \cdot \sum_{X}^{X+365} (1 - \mu_{IP})^{X}, \tag{6.6}$$

$$ERS_{TTP} = N_{IP} \cdot \bar{F} \cdot [(1 - P) + P \cdot (1 - Z)] \left[\sum_{X+365}^{X_{max}} (1 - \mu_{IP})^{X} \right], \tag{6.7}$$

where X is the age of sex change, X_{max} is the maximum longevity, and μ_{TP} the daily mortality rate. N_{IP} represents the mating success expressed as number of pair-spawning day^{-1}. $\bar{F}$ is the fecundity of an IP of average age estimated using the relationship described above. The average age of an IP female in our population is estimated form the age structure (Fig. 6.2d). A TTP loses part of the paternity in some of the pair-spawning due to streaking. The streaking rate (P) at our study population is 32% (Chapter 7). The paternity loss due to sperm competition (Z) is assumed to be 50%. This estimation is based on the study of Wooninck et al. (2000) who report a 50% paternity loss due to streaking for the territorial male of the wrasse *Thalassoma bifasciatum*.

The age at which the ERS_{IP} equals ERS_{TP} is the threshold value beyond which sex change should not occur. Thus, sex change is not expected to occur for the following condition:

$$ERS_{IP} \geq ERS_{TP}, \tag{6.8}$$

Confidence bands for the *ERS* estimates of IPs and TPs were constructed by incorporating variation to the mortality estimate. Mortality values were simulated (1000 simulations) assuming a normal distribution and the mean and standard error values given in Table 6.2. All other model parameters were kept constant. Upper and lower bounds of *ERS* for each age were estimated using the percentile method. The confidence bands in this case give the possible boundaries of *ERS* given the estimated variation in morality rate of the study population. A further study of the effect of higher male mortality on the *ERS*, was conducted by varying the mean male mortality rate. The female mortality was fixed and the male mortality varied to give a male:female mortality ratio ranging from 1:1 to 1:2. The *ERS* and the threshold age of sex change were estimated for each of these mortality ratios and for different mating successes.

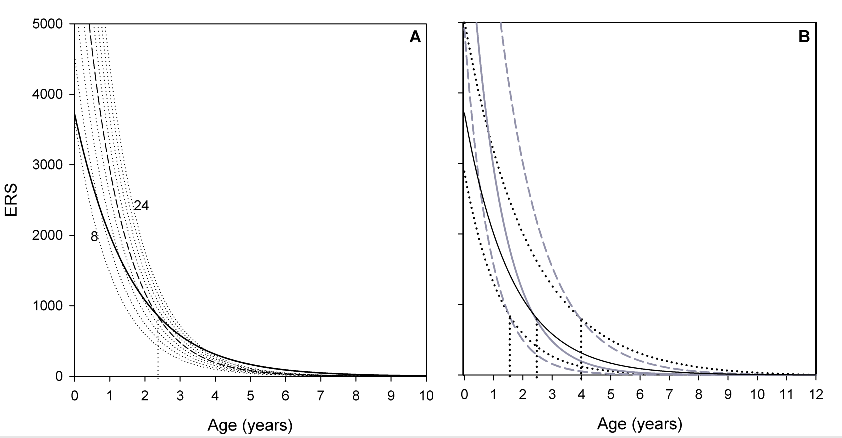

Fig. B6.1.1 *Scarus ferrugineus*. (A) The expected reproductive success (*ERS*) of an initial phase female (IP female) (solid line) and terminal phase male (TP) (dotted/dashed lines). The *ERS* of a TP is shown for different mating successes ranging from 8 to 24 pair-spawning day^{-1} with an increment of 2. The dashed line is the *ERS* for the maximum observed mating success in our study population of *S. ferrugineus* i.e. 16 pair-spawning day^{-1}. Vertical dashed line is the threshold age beyond which an individual should not change sex if its maximum mating success as a TP is 16 pair-spawning day^{-1}. (B) The mean *ERS* of IP females (black solid line) and 95% confidence bands (black dotted lines). The mean *ERS* of a TP (grey solid line) and 95% confidence bands (grey dashed lines). Vertical dotted lines are lower, mean and upper bounds of the threshold age of no sex change.

Results and discussion

The *ERS* of an IP and a TP *S. ferrugineus* declines with age due to mortality (Fig. B6.1.1). For TPs the *ERS* is a function of the daily mating success, with the *ERS* at a given age steadily increasing as the mating success increases (Fig. B6.1.1). Recall that, the decision to change sex at a certain age depends on whether the individual will have a higher *ERS* as a sex-changed individual or as a female. Thus, for all the ages where the *ERS* of TPs is above that of the IPs in Fig. B6.1.1, sex-change is predicted to occur. The effect of mating success (pair-spawning day^{-1}) on the threshold age of sex change is depicted in the phase diagram (Fig. B6.1.2). With increasing mating success, the threshold age of sex change increases. Thus with a mating success of 24 an individual can continue to change sex up to a maximum age of 4 years. While with a mating success of 16 the individual should not change sex beyond 2.5 years.

For the parameter values of *S. ferrugineus* the model predicts sex change should occur at any age if the male and female mortalities are equal (Fig. B6.1.2B). When male mortality is higher, sex change beyond certain ages leads to lower *ERS* than when the individual had stayed female. Predictably, increase in the mating success causes the threshold age of sex change to increase.

The simulated lower and upper boundaries of the threshold age of no-sex change for our population are 1.5 and 4 years (Fig. B6.1.2B). If the predictions of the model are correct, then newly sex-changed individuals older than the upper threshold limit should be rare in our population. We tested this by looking at the age distribution of small TPs of size 15 – 27 cm. Since this size range overlaps with that of the IPs, these TPs are expected to be newly sex changed individuals. Frequency distribution of the age shows that 83% of these small TPs lie within the predicted bounds of the threshold age of sex change (Fig. B6.1.3), confirming the model predictions.

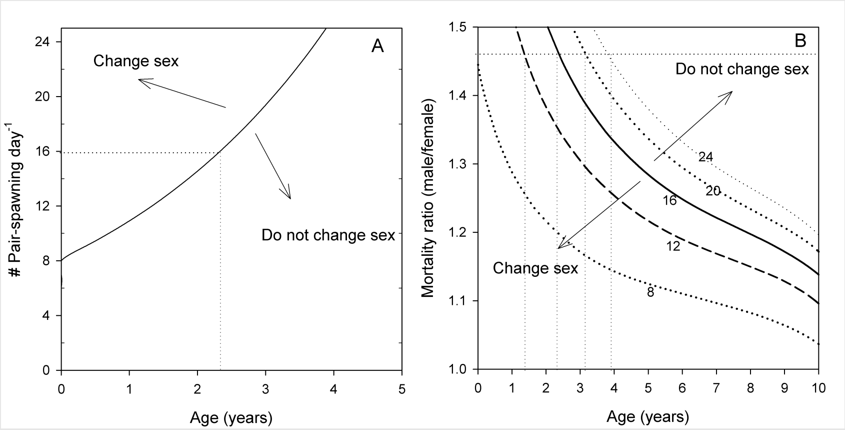

Fig. B6.1.2 *Scarus ferrugineus*. Phase diagrams of the decision to change or not to change sex. (A) The effect of the mating success (# pair-spawning day^{-1}) and age. Predicted upper threshold age (beyond which there should not be sex change) for our study population's maximum observed mating success is shown in dotted lines. (B) The effect of: ratio of male:female mortality, age, and mating success (# pair-spawning day^{-1}) on the decision to change or not to change sex. Numbers on curves are the mating success of terminal phase males (TPs). Dotted horizontal line is the TP/IP mortality ratio of our study population of *S. ferrugineus*. Dotted vertical lines show – for different mating success rates - threshold ages beyond which there should not be sex change.

Previous research has suggested that size-fecundity skew, i.e. the disproportionate contribution of large females to the collective fecundity of a harem explains the existence of large none-sex changing females (Munoz & Warner 2003b; Munoz & Warner 2004). In this case, if the fecundity of a large female is greater than the collective fecundity of its harem members, changing to male for this female means fertilizing fewer eggs than she could produce as a female. Therefore this individual does better by staying female while a subordinate individual changes sex. However, this model considers the situation at one point in time i.e. at the time of the demise of the dominant male and does not take account of the role of growth and mortality (Munoz & Warner 2003b). For example, if we consider the fast growth rate of parrotfishes (van Rooij et al. 1995b; Choat et al. 1996), and estimate *ERS* over a period of one year, then a sex-changed individual will surely gain much more due to the growth in size of its harem members. Higher male mortality by discounting the *ERS* of a sex-changed individual will have the opposite effect of growth. A further limitation of the model is that it is inapplicable to lek-like mating systems. In leks, size-fecundity skew is unlikely to have similar influence as in harems, due to the open nature of the former reproductive system.

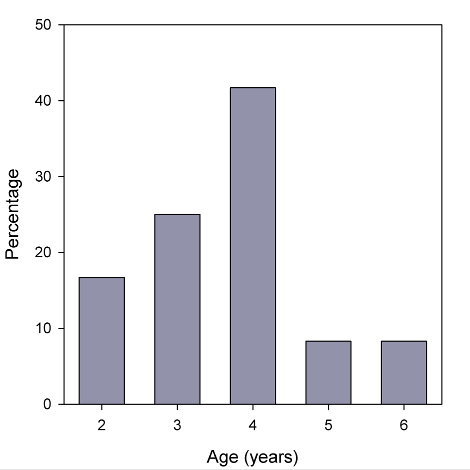

Fig. B6.1.3 *Scarus ferrugineus*. Age distribution of small TPs (15 – 27 cm fork length) captured at the study site.

In this study, a combination of detailed information on mating tactics, and demography made it possible to use a simple mechanistic model to predict patterns of sex change in *S. ferrugineus*. The results demonstrate that higher male mortality sets an upper threshold age beyond which sex change will not be beneficial in a lekking species. Clifton and Rogers (2008) have suggested that even in haremic species higher male mortality alone can lead to large/older non-sex-changing females. No sex-change by older females is congruent with the widely accepted view of the variability of sex-change (Munday et al. 2006; Munday et al. 2006). Indeed sex change is highly flexible and is influenced by the prevailing social and demographic conditions (Shapiro & Lubbock 1980; Shapiro 1980; Munday et al. 2006; Molloy et al. 2011). If the right social and demographic cues for sex change are not met, a female may pass beyond the threshold age. The old non-sex-changing females in *S. ferrugineus* are therefore individuals who have crossed the threshold age without experiencing social and demographic cues to change sex.

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CHAPTER 7

BREEDING STRATEGIES OF THE PARROTFISH *SCARUS FERRUGINEUS* IN THE SOUTHERN RED SEA

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Abstract Coral reef grazers living in seasonal habitats such as the southern Red Sea face seasonal variation of the availability and nutritional quality of food resources. The influence of this variation on the population ecology of grazing fish is rarely studied. In this work we investigate the timing of spawning of the rusty parrotfish *Scarus ferrugineus* using behavioral observations of focal animals in the field and by monitoring gonad development and body condition. Behavioural observations of spawning behaviour as well as gonad mass and oocyte development show that spawning takes place throughout the year. The spawning intensity differs significantly between seasons. During the cooler season gonads are more developed, a higher percentage of females are ripe (contain hydrated oocytes), and spawning related behavioural interactions such as territory defence and courtship are more intense. Also the duration of the spawning period is longer and more individuals participate in spawning activities which leads to territorial males keeping significantly smaller territories. The timing of recruitment reflects the seasonal pattern of spawning with a time lag of about 1 – 2 months. There is seasonal variation in body condition and liver mass. In the hot season body reserves and gonad mass are positively correlated implying that concurrent food intake supplies the energy for gonad growth. In the cool season *S. ferrugineus* uses a capital breeding strategy since body reserves decline during this peak reproductive season indicating that these are used for reproduction. Capital breeding strategy by *S. ferrugineus* in the cool season appears to be an adaptation to avoid trade-off between feeding and spawning.

To be submitted

7.1 Introduction

The manner in which organisms allocate resources to competing processes such as growth and reproduction is the central theme of life-history strategies (Stearns 1992). When resources vary temporally, the decision whether to grow or to reproduce during the season of resource abundance (the vegetative season) can have profound effects on the fitness of indeterminate growers such as fish (Ejsmond et al. 2010). On the one hand, theory suggests that indeterminate growers can maximize their fitness by timing their reproduction at the end of the vegetative season (Stearns 1992). By devoting resources to growth individuals will increase in size and hence gain higher fecundity. On the other hand, offspring produced early in the vegetative season has the highest chances of survival (Cargnelli & Neff 2006; Varpe et al. 2009). This is partly because larvae and juveniles can utilize the abundant resources available during that season. Offspring spawned early in spring will achieve bigger size and store more energy providing better survival chances during the winter season (Post & Evans 1989). This is the classic match-mismatch hypothesis (Cushing 1975), where spawning is timed to ensure optimal conditions for the larvae. Empirical evidence suggests that most marine fishes living in seasonal habitats adopt the latter (Qasim 1956; Cushing 1975).

In order to be able to spawn early in the vegetative season, fish need to utilize energy stored from the previous year (Varpe et al. 2009). Storage of energy allows fish to relocate energy from times of resource abundance to times that maximise offspring survival (Reznick & Braun 1987; Varpe & Fiksen 2010). This strategy known as "capital breeding" (sensu, Drent & Daan 1980) is prevalent among ectothermic organisms especially those from seasonal environments (Jonsson 1997; Bonnet et al. 1998). The opposite strategy is "income breeding" in which organisms utilize concurrent energy intake for reproduction and is expected to be prevalent in temporally predictable habitats (Jonsson 1997).

In capital breeders, the quantity of the stored energy is an important indicator of the reproductive status (Drent & Daan 1980; Lourdais et al. 2002; Alonso-Fernandez & Saborido-Rey 2012). Indeed fish with higher energy reserves produce more gametes (Kjesbu et al. 1991; Lambert & Dutil 2000), may mature earlier (Morgan 2004) or are less likely to skip a spawning season than fish in poorer condition (Rideout et al. 2000; Jorgensen et al. 2006). Moreover parental investment in the form of egg yolk is higher in mothers in better condition resulting in increased growth and higher survival of larvae and juveniles (McCormick 2003; Donelson et al. 2008; Samhouri 2009).

Seasonal and spatial variability of food resource abundance is a common feature of many natural habitats including marine ecosystems. Even tropical ecosystems such as coral reefs experience seasonal variation in resources (Hatcher 1997; Kleypas et al. 1999a; Bruno et al. 2009). In particular reefs located at continental margins or in monsoon influenced regions are typically characterized by seasonal changes in water currents, upwelling, river input and precipitation (McClanahan 1988; Ormond & Banaimoon 1994; Ateweberhan et al. 2006a). Benthic algae on these reefs show seasonality in biomass, species composition and nutritional value (Diaz-Pulido & Garzon-Ferreira 2002; Ateweberhan et al. 2006a; Lefevre & Bellwood 2011). For example turf algae - the prime food source of many reef grazers - have higher production in the summer season due to the capacity to tolerate high temperature and light levels (Carpenter 1985; Klumpp & Mckinnon 1992; Ateweberhan et al. 2006a; Copertino et al. 2009).

Coral reef grazers respond to these seasonal changes in resources by altering food preference and/or daily energy intake rates (Fishelson et al. 1987; Kennish 1997; Letourneur et al. 1997; Ferreira et al. 1998; Hernaman et al. 2009; Afeworki et al. 2011). Coral reef grazers are therefore likely to face periods of surplus energy as well as lean seasons in which the daily energy intake may not balance the expenditure. Indeed seasonality in body energy reserves in reef grazers are known from acanthurids (Fishelson et al. 1987; Montgomery & Galzin 1993), parrotfishes (van Rooij et al. 1995a), and rabbit fishes (Hanna 1984; Ntiba & Jaccarini 1990). Moreover seasonal change in growth is known from coral reef fishes (Pauly & Ingles 1982; Longhurst & Pauly 1987; van Rooij et al. 1995b, Chapter 5).

Temporal and spatial fluctuation of fish body condition is likely to influence the timing of reproduction, fecundity and recruitment success of reef fishes (Clifton 1995; Jones & McCormick 2002; Samhouri 2009). This view is supported by widespread records of spawning seasonality in reef fishes (Thresher 1984; Ntiba & Jaccarini 1990; Robertson 1991b; Claydon 2005; Grandcourt et al. 2007). Even reef fish species that spawn throughout the year tend to have seasons of peak spawning activity or high fecundity (Colin 1978; Craig 1998; Bushnell et al. 2010; Lowerre-Barbieri et al. 2011). Nevertheless the connection between reproductive seasonality, resource availability and fish body condition is rarely made (Clifton 1995). Part of the reason is the still widely accepted view of stability in environmental conditions of reefs. Also, the predominant view that timing of reproduction in reef fishes is primarily adapted to increase larval survival has tended to shift focus on pelagic processes rather than on the adult population (Doherty & Williams 1988; Robertson 1991b; Jones & McCormick 2002). To what extent adult biology influences reproductive decisions has - by comparison - received little attention (Robertson 1991b; Clifton 1995). Works investigating spatial and temporal patterns of food resources and their impact on reproduction have however questioned this and have highlighted the influence of adult condition on reproductive and recruitment success (see Jones 1991; Jones & McCormick 2002 for reviews).

The highly seasonal character of the southern Red Sea renders it suitable to investigate how varying resource levels influence the timing of reproduction in reef fishes (Afeworki et al. 2013). This region is strongly influenced by the Indian monsoon and has two distinct seasons – the cool and the hot seasons (Sheppard et al. 1992). The phenology of erect macroalgae and crustose corralines varies from a cool season maximum of growth, biomass and reproductive activity to a hot season minimum (Ateweberhan et al. 2005a, 2006b,a). Turf algae show opposite seasonality, with peaks of cover and biomass occurring in the hot rather than in the cool season (Ateweberhan et al. 2006a; Afeworki et al. 2011).

Using a common coral reef grazer (*Scarus ferrugineus*) as a model animal, we investigate how its reproductive ecology of is influenced by fluctuations in environmental conditions. *S. ferrugineus* is a benthic feeder that scrapes turf algae and associated detritus from coralline substrates (Afeworki et al. 2011). Its habitat use, feeding preferences, daily intake rate and growth is influenced by the seasonality in environmental conditions (Afeworki et al. 2011; 2013; 2013). The social structure and mating tactics of *S. ferrugineus* are reported in Chapter 8

7.2 Materials and Methods

7.2.1 Study site and environmental parameters

Fish collection was conducted at the fringing reef of Sheikh Said Island near Massawa, Eritrea. The southern Red Sea experiences two monsoon driven distinct seasons. The cool season lasting from December – April is characterized by low temperatures (average 27°C), south-easterly winds, more cloud cover and low irradiation. The hot season extends from June – October and is known for its high temperatures (average 34°C), north-westerly winds and high irradiation. Benthic algae of this area are greatly influenced by this seasonality. Macroalgae such as *Sargassum* and *Turbinaria*, foliose and crustose corallines proliferate during the cool season in the shallow reef zones (Ateweberhan et al. 2005a, 2006a,b, 2008). These die during the hot season and the exposed space is overtaken by turf algae (Ateweberhan et al. 2006a; Afeworki et al. 2011). As a result the availability of turfs growing on endolithic algae, the preferred grazing substrate of *S. ferrugineus*, is at its peak during the warmer parts of the year (Afeworki et al. 2011).

7.2.2 Study species

Scarus ferrugineus is a diandric protogynous hermaphrodite (Abdel-Aziz et al. 2012) endemic to the Red Sea and the Arabian Sea (Randall & Ormond 1978; Randall 1983). *S. ferrugineus* like most other protogynous labrids has two life phases: the initial phase (IP) and the terminal phase (TP). IP individuals (IPs) are yellow brown in colour with the caudal part and the fins being more yellowish. IPs are largely female with about 5% of them being primary males (here referred to as IP males) (Abdel-Aziz et al. 2012, Chapter 8). TP fish (TPs) are brightly coloured with much of the body being blue with purple and green streaks. Within its range *S. ferrugineus* is one of the most abundant grazers and at the current study site it is the dominant grazer in terms of biomass (Afeworki et al. 2013). *S. ferrugineus* feeds on turfs throughout the year and has a strong preference for turfs that grow on endolithic algae (Afeworki et al. 2011).

7.2.3 Measurement of environmental parameters

Air temperature (°C), wind speed (km h^{-1}), gust speed (km h^{-1}) and photosynthetically available radiation (PAR) (μEm^{-2} d^{-1}) were recorded between 2006 – 2008 using a weather station (HOBO onset technologies) mounted 2 m above ground level at a location 1 km away from the study site. Water temperature was recorded at 2 m depth on the shallow fore reef zone of Sheikh Said Island from 2003 – 2006 on an hourly basis. Estimates of pelagic productivity were compiled for grids close to the study site from the Joint Research Centre-European Commission (http://gmis.jrc.ec.europa.eu).

7.2.4 Body condition and gonad development

Monthly samples of five IPs and five TPs were collected from January 2006 to May 2007 by spearing. Each fish was put in a separate plastic bag and put in a box with ice flakes until they were transported to the laboratory where they were stored in freezers at -30°C before processing. Dissections were conducted within a period of one month after capture. The life phase, fork length (from the tip of the snout to the fork in the tail), body depth, and whole body mass were recorded prior to dissections. Both the gonad pair and the liver were extracted and the wet mass measured to the nearest 0.001 g on an electronic scale. The left and right otoliths were extracted for age determination (see Chapter 6 for details). Since the IPs could either be female or male, the sexual identity of each IP was determined by visual inspection of the gonads and later ascertained by examination of histological preparations.

Body condition: The gut along with its food contents were excised and used for another study investigating the feeding ecology of the species (Chapter 4). The body dry mass (DM) and body condition estimates reported here therefore refer to fish whose intestine, liver, gonad and otoliths were removed. Effect of the exclusion of the gut from the analysis of seasonal changes in body condition of the species was assumed to be minimal. Unlike some acanthurids where a substantial part of their energy reserve is stored in mesenterial filaments of the gut or retroperitoneal fat bodies (Fishelson et al. 1985; Montgomery & Galzin 1993), there were no such fat deposits around the intestine of *S. ferrugineus*. This was ascertained by careful visual examination of the viscera of over 300 individuals during different seasons. DM was estimated by drying specimens at 110°C for 24 hours and weighing to the nearest 0.1 g. Since fish are known to compensate declines in body fat and protein with water (Weatherley & Gill 1987; Murchie et al. 2010), DM is a more accurate indicator of body condition than wet mass (Murchie et al. 2010; Alonso-Fernandez & Saborido-Rey 2012). In this study comparison of body condition among months was therefore conducted using DM of gutted individuals instead of wet mass.

Histology: Of all collected gonads, approximately half were preserved in a 4% seawater and formalin solution for histological examination (Table 8.1). Ovary/testis tissue was dehydrated in a series with increasing concentrations of ethanol. Subsequently, after clearing in xylene, the tissue was embedded in paraffin and thin sections were cut on a microtome. For each fish, at least two transverse sections from the central part of the ovary/testis were mounted on microscopic slides and stained using hematoxylin/eosin. Non-uniform distribution of oocyte developmental stages in different regions of the ovary can introduce bias if examination is done in one region alone. However comparison of gonad sections from a large number of teleosts (see West 1990) including labrids (Coulson et al. 2009; Muncaster et al. 2010) has shown that oocyte development is uniform along the ovary. Given this, we expect our sections from the mid-region to be representative of the whole ovary.

All histological procedures were conducted at the Central Laboratory (Histological Lab) of Orota Hospital, Asmara, Eritrea. High resolution digital photographs of each section were taken through a microscope at 100 times magnification. Four oocyte developmental stages were identified (West 1990; Tyler & Sumpter 1996).

1. *Primary growth stage*: Gonads have the smallest oocytes, staining dark in hematoxylin. The oocytes have a large nucleus and a thin sheath of cytoplasm. This stage is further characterized by the development of the Balbiani body (a heterogeneous group of organelles in the cytoplasm) and the zona radiata (an acellular vitelline envelope). Towards the end of this stage multiple nucleoli appear around the large nucleus.

2. *Cortical alveoli stage*: During this stage the cytoplasm starts to harbour cortical alveoli which contain glycoproteins whose function is to prevent polyspermy by hardening the theca after fertilization. Towards the end of this stage the cortical alveoli migrate to the periphery while the central part is filling with yolk globules.

3. *Vitellogenic stage*: The bulk of oocyte growth occurs during this stage which is reflected in the rapid increase in gonad mass. Vitellogenin (precursor of yolk proteins) derived from the liver is sequestered and processed to form the granules filled with yolk proteins.

4. *Mature stage*: This is the final developmental stage of the oocyte prior to being released into the ovarian lumen. This stage is characterized by the migration of the nucleus to the animal pole and the dissolution of its membrane. The yolk granules may coalesce making the cytoplasm look more transparent. In pelagic spawners hydration is the final phase of maturation which enables the production of buoyant oocytes.

Studies of fish reproduction usually classify ovaries based on the most advanced oocyte present in the histological section (West 1990). Point-count technique - usually using a sampling grid - is a quantitative and accurate albeit time consuming way to estimate the areal fraction (henceforth proportion) of oocyte developmental stages (Coward & Bromage 2002a). In this study we use line-intercepts (instead of grid points) to quantify the proportion of oocytes at each developmental stage. Two lines perpendicular to each other were drawn on the digital image of each section and the length of each oocyte intercepted by the lines was measured using the freely available image analysis software ImageJ version 1.44 (http://imagej.nih.gov/ij/). Proportion of each oocyte developmental stage was estimated as the sum of the lengths intercepted by this stage divided by total length of the transect. In addition, a grid of at least 100 points was placed on each section and the proportion of each stage determined. Chi-square goodness of fit tests between estimates of the transect method and grid method showed that the two methods give similar result ($\chi^2 : P \gg 0.05$). In 10% of the sections results from the two approaches differed ($\chi^2 : P < 0.05$). Therefore, the mean of the estimates from both methods was used for the final analysis.

Stripping of ripe females: As part of a study investigating the growth of *S. ferrugineus* using tagging techniques, females were stripped to check if they were ripe or not. See Chapter 6 for details of the capturing technique and the general treatment of the fish. Briefly, females were captured and kept in perforated tanks within their habitat overnight. The next morning each female was anesthetized using clove oil and the belly was gently squeezed to check for hydrated eggs. Individuals with hydrated oocytes were assumed to be ready to spawn within that day. The percentage of females with hydrated oocytes (henceforth ripe females) is used as an indicator of the proportion of females being engaged in the daily reproductive effort.

7.2.5 Field observations of spawning in *Scarus ferrugineus*

To describe the mating tactic and to determine the timing of spawning in *S. ferrugineus*, field observations on territorial males were conducted from August 2007 – June 2008. Observations were conducted by SCUBA for 4 – 11 days of each month to record incidence of spawning, measure the width of spawning territories, and the number of individuals participating in these spawning events.

Incidence of spawning: In the early stages of the study (January 2006 – August 2007), daily dives were undertaken at different times of the day to determine the location and the diurnal timing of territoriality and spawning. During each dive, the reef zones were inspected for the occurrence of territorial activity. After over one year of exploratory dives it was ascertained that territorial TPs (TTPs) keep contiguous temporary spawning territories at the deep fore reef. Spawning was recorded mostly during the morning hours. However the exact time of the start and end times of the spawning appeared to vary with season and tidal phase. Owing to this variation, the spawning territories were visited daily to check for the occurrence of territorial behaviour. Once territorial behaviour is detected, detailed observations were made by two divers on two different target TTPs. During each observation the frequency of occurrence of the following activities were recorded:

a. *Broadside view*: involves full erection of all fins in particular of the dorsal and caudal fins followed by zigzag swimming. This behaviour is often elicited when two neighbouring TTPs come close at their common border.

b. *Chasing*: when the TTP uses both the pectoral and caudal fins to rush at and drive intruding IPs or TPs beyond the territory. In this case the target usually swims away fast by using both the caudal and pectoral fins.

c. *Courting*: when the TTP swims in an oblique body position circling an IP entering the territory. During this circling the TTP uses only the pectoral fins, occasionally rushing up into the water column several times. During rushes the TTP uses the caudal fin. An IP may spawn with the current TTP or may leave the territory to the adjoining territory.

d. *Spawning*: when a TTP and an IP swim side by side before rushing into the water column to release gametes. Spawning usually follows courting. The spawning ascent of *Scarus ferrugineus* is brief lasting only a few seconds.

Finally the incidence of egg predation by planktivores and predation attempts on the spawning pair by large piscivores was recorded. Observations were initiated as much as possible at the onset of territoriality and were continued until the TTP left its territory. As the onset of spawning activity was variable, this was often impossible to accomplish. Moreover, due to the limitations of diving time, continuous observation during an entire spawning period was not always feasible, especially during the cold season when spawning could last up to 3 hours. To account for these limitations, the number of spawning events per TTP per day was quantified as the product of the mean spawning rate per minute and the maximum duration of spawning period recorded for each month (following van Rooij et al. 1996a). This gives the maximum number of spawning events TTP^{-1} day^{-1} for each month. A second and more conservative estimate was calculated as the product of the mean spawning rate minute^{-1} and the mean duration of spawning of each month. The latter gives the average number of spawning events TTP^{-1} day^{-1} for each month.

Density of spawners: the number of participants in a spawning aggregation is an indicator of the intensity of the spawning at a given month. Density of spawners was estimated by underwater visual census conducted on the deep fore reef along three permanent 30 m transects. Fish encountered within 2.5 m on either side of transects were counted and assigned to predefined categories, IP, TTP, and TP. Furthermore the area of the reef occupied by a single TTP was measured as an indicator of the spawner density. The area per TTP is expected to vary with density and competition for spawning space (Hixon 1980; van Rooij et al. 1996a). In *S. ferrugineus* the territory width is sufficient to quantify the area occupied by a TTP since the territories appear to have no borders on the deeper and shallower sides. The TTPs moved freely to the shallow as well as to the deeper part of their strip. Laterally however, their territory is delimited by a neighbouring TTP on either side. Territory width was defined as the extreme lateral points where a TTP regularly visited without being repulsed by the neighbouring TTPs. If two TTPs happen to be close to their common border, they typically responded by stretching all their fins and displaying the broadside of the body before they parted to their respective territories. The territory borders are therefore the zones of interaction between neighbouring TTPs. Markers (metal sinks with brightly colored floats) were dropped at these extreme points and the lateral distance (m) between these points was measured using a measuring tape.

7.2.6 Temporal and spatial trends in recruitment

Monthly counts of recruits of *S. ferrugineus* were conducted between 2006 and 2008 on the reef flat (0 – 1 m), the reef crest (0 – 2 m), the shallow fore reef (2 – 6 m), and the deep fore reef (6 – 10 m). A description of the reef zones and the vertical profile of the reef is provided in Chapters 1, 2, and 3. In each reef zone six 30 m transects were haphazardly placed along the same depth and were permanently fixed with metal stakes (Afeworki et al. 2013). Recruits encountered 1 m on either side of each transect were tallied into five 2 cm size classes (0 – 10 cm). The 0 – 2 cm size class represents the new recruits that settled within the month of counting (Paddack & Sponaugle 2008).

7.2.7 Data analysis

Temporal trends in DM, gonad mass and liver mass were investigated using analysis of covariance (ANCOVA). The gonadosomatic index (GSI), the hepatosomatic index (HIS) and the Foulton condition factor (K) are still widely used in studying temporal trends in somatic and reproductive condition in fish (Packard & Boardman 1999). Many researchers have warned for a cautious application of these indices and recommend the use of ANCOVA (Garcia-Berthou & Moreno-Amich 1993; Packard & Boardman 1999; Ebert et al. 2011) since these indices are not independent of the body length and may give misleading results. ANCOVA offers a statistically valid means to estimate the mean monthly mass (e.g. of liver or gonad) for a fish of fixed length thus controlling for the effect of the body size.

Monthly differences in frequency minute^{-1} of spawning, courting, broadside view, chasing were tested using ANOVA. The proportion of oocytes in the advanced stages of development (vitellogenic + mature) was regressed with wet gonad mass and the best model was selected based on the R^2 value and the Akaike Information Criterion (AIC). Using the selected model the proportion of oocytes in the advanced developmental stage was estimated for the ovary samples which were not processed histologically. MDS plots and similarity contours derived from cluster analysis were used to classify males based on testis mass and fork length. Differences in recruit density among zones and months was investigated using generalized mixed linear models with log-link and assuming Poisson distribution (GLMM). The zero-inflated model in the statistical package SAS (SAS 2006) was employed to account for the large number of zero counts in the data. Monthly differences in mean density of spawning fish and differences in mean number of fish between spawning and none-spawning periods at the deep fore reef were tasted using ANOVA. Similarly, the width of territories of TTPs across months was compared using ANOVA. Prior to performing parametric tests, the data was assessed for normality using Kolmogorov-Smirnov goodness of fit test and for homogeneity of

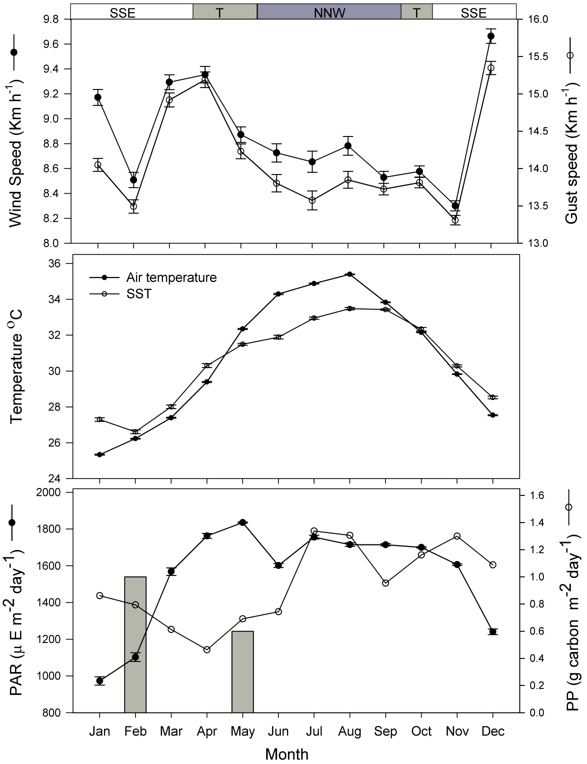

Fig. 7.1 Massawa, southern Red Sea: Mean monthly trends in environmental conditions near the study site. Air temperature and sea surface temperature (SST) are measured from the study site. PAR: photosynthetically available radiation; PP: pelagic primary production. Bars: *in situ* PP measurement on two southern Red Sea Sites May 1992 and Feb 1993 taken from Veldhuis et al. (1997). Monsoon cycle and wind direction indicated on bar on top. SSE: north-east monsoon (cool season). NNW: south-west monsoon (hot season). T: transition periods with variable winds.

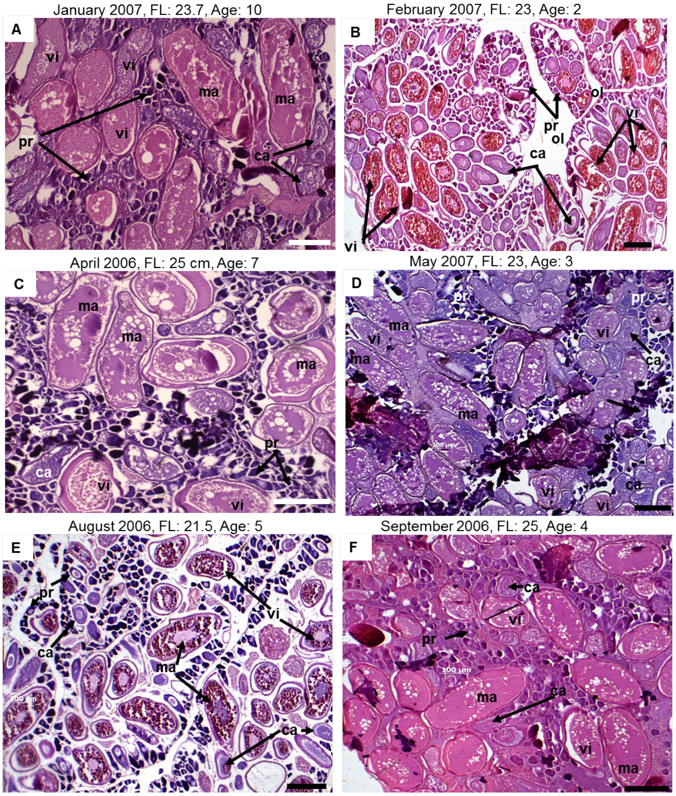

Fig. 7.2 *Scarus ferrugineus*. Histological sections of gonads from different months showing the presence of advanced ooctes (vitellogenic + mature) throughout the year. **pr**: primary growth oocytes, **ca**: cortical alveoli oocytes, **vi**: vitellogenic oocytes, **ma**: mature oocytes. Scale bar at bottom right corner = 200 μm

variance using Levene's test. Most of the data met the requirements for parametric tests with the exception of the testis mass and liver mass (IPs) both of which were log transformed before the analysis.

7.3 Results

7.3.1 Environmental conditions at the study site

Conditions at the study site are clearly monsoon influenced. During the south-easterly monsoon, the area is characterized by higher wind speeds, low temperature and low PAR values (Fig. 7.1). The south-western monsoon has calm seas, high PAR values and high SST. Pelagic production has a significant seasonal trend with highest primary production during hot season (Fig. 7.1).

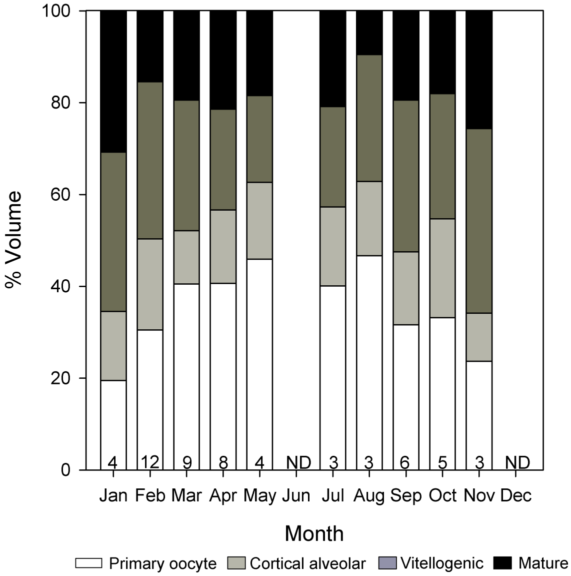

Fig. 7.3 *Scarus ferrugineus*. Bar graph: Monthly changes in the proportion of oocytes at different developmental stages. ND: no data.

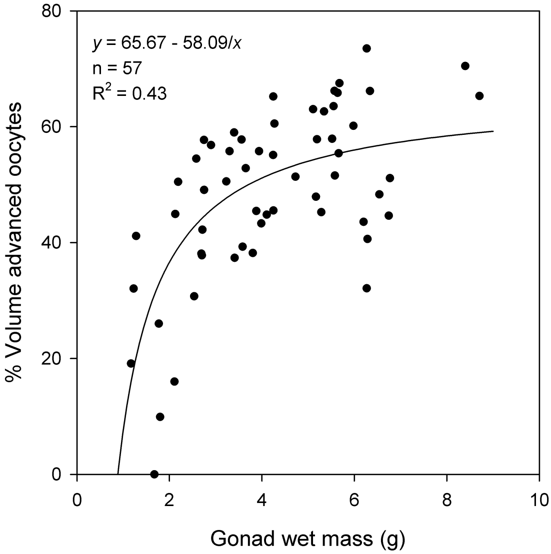

Fig. 7.4 *Scarus ferrugineus*. Relationship between the proportion of oocytes in advanced developmental stages (vitellogenic + mature) (y) and ovary wet mass (x).

7.3.2 Dry mass, liver mass, gonad mass and oocyte development

Ovary and testis wet mass of *S. ferrugineus* showed significant monthly variation with similar temporal dynamics (Table 7.1, Fig 7.5). Both ovary and testis mass peaked during the cool season from November – March and the lowest values were recorded around June – August (Fig. 7.5A). All oocyte developmental stages were prevalent throughout the year in ovary sections of *S. ferrugineus* (Fig. 7.2 & 7.3). Moreover, all examined IPs contained vittelogenic and mature oocytes and hence are by definition "mature" (Murua et al. 2003). This is to be expected as we have sampled only the adult population with fork lengths of 20 – 26 cm. The proportion of oocytes in different stages of development showed significant monthly variation (Fig. 7.3). Oocytes in an advanced stage of development (vitellogenic + mature) were most common in the cool months (November – February), occupying 50 – 65% of the ovary volume (Figs. 7.3 & 7.5A). Similar values were recorded in September where advanced oocytes occupied 52% of the ovary volume (Figs. 7.3 & 7.5A).

Table 7.1 *Scarus ferrugineus*. Summary of ANCOVA tests of the monthly trends in dry body mass, liver mass and gonad/testis mass of IP and TP fish.

	Factor	Dry body mass			Liver wet mass			Gonad/testis wet mass		
		df	*F*	*P*	*df*	*F*	*P*	*df*	*F*	*P*
IP	Intercept	1	422.14	0.00	1	16.15	0.00	1	3.97	0.05
	Fork length	1	1553.62	0.00	1	35.66	0.00	1	9.57	0.00
	Month	10, 115	16.82	0.00	10,112	41.00	0.00	10,115	5.80	0.00
TP	Intercept	1	202.86	0.00	1	0.85	0.77	1	0.12	0. 73
	Fork length	1	847.04	0.00	1	0.70	0.41	1	0.00	0.99
	Month	10,81	4.53	0.00	10,80	10.98	0.00	10,80	9.91	0.00

The proportion of advanced oocytes was positively related to ovary wet mass and the relationship fitted a Michaelis-Menten type curve best (Fig. 7.4). Using this relationship, the proportion of advanced oocytes of ovaries that were not examined histologically was calculated; the result (Fig. 7.5A) confirms the seasonality outlined above. The proportion females that were ripe was highest during the cool season (Fig. 7.6) suggesting that more females tended to participate during the daily spawning event in the cool compared to the hot season. In summary, oocytes in advanced developmental stages occur throughout the year but their volume proportion is higher in September and during the cooler months and is lowest in June.

DM and liver mass in IPs and TPs showed significant seasonal change (Table 7.1; Fig. 7.5B, C). Both variables had similar temporal trends rising from the lowest values in May – June to peak values in November. The decline in liver mass from the peak value in November starts in the cool season in January reaching its nadir in April (Fig. 7.5B). This decline is steeper in IPs than in TPs. DM declines from its peak in November through the cool period and reaches its lowest value one month after liver mass has reached minimum values (Fig. 7.5C).

Testis mass in TPs is negatively correlated with liver mass (Pearson correlation: $R^2 = -0.425$, $P = 0.000$, n = 74) and DM appeared to be positively correlated with liver mass (Pearson correlation: $R^2 = 0.28$, $P = 0.02$. n = 73). However there was no correlation between DM and

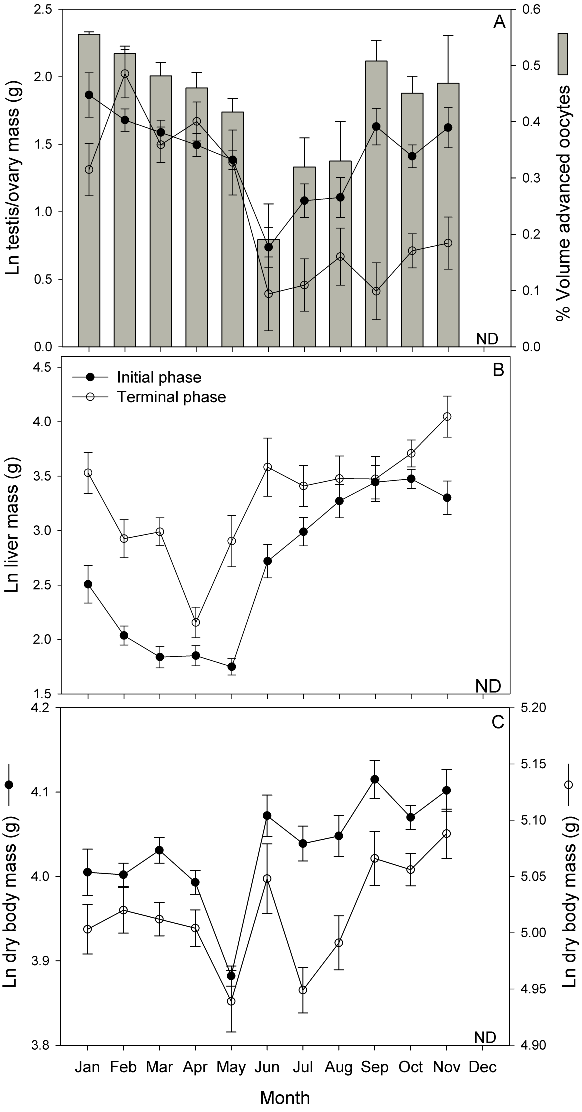

Fig. 7.5 *Scarus ferrugineus*. (A) Mean monthly variation in ovary and testis mass. Bars show the proportion of advanced oocytes (vitellogenic + mature) calculated from ovary wet mass. (B) Mean monthly liver mass and (C) body mass of initial phase and terminal phase individuals. Monthly means are estimated for a 23 cm IP fish and a 34 cm TP from the ANCOVA model. ND: no data.

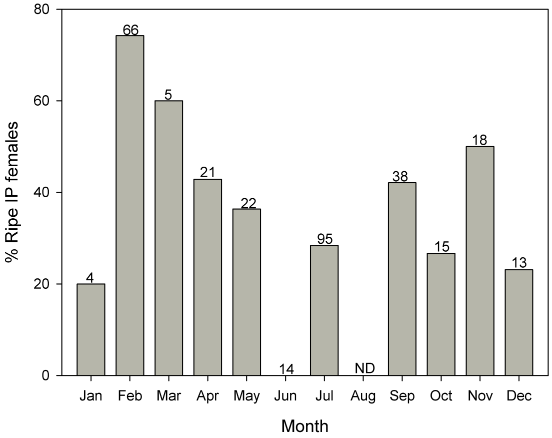

Fig. 7.6 *Scarus ferrugineus.* Monthly trend in the percentage of females engaged in the daily spawning event. Numbers above bars are number of females stripped in the field. ND: no data.

testis mass (Pearson correlation: $R^2 = -0.01$, $P = 0.941$. n = 74). In IPs, ovary mass was positively correlated with DM (Pearson correlation: $R^2 = 0.32$, $P = 0.000$. n = 116) while there was no correlation with liver mass (Pearson correlation: $R^2 = 0.07$, $P = 0.45$, n = 114). Liver mass and DM were positively correlated (Pearson correlation: $R^2 = 0.61$, $P = 0.000$. n = 113). The lack of correlation between ovary and liver mass in IPs stems from the none-linear v-shaped trends of the two (Fig. 7.5). From June – September both are increasing (Pearson correlation: $R^2 = 0.43$, $P = 0.00$. n = 43) and from January – May both are declining (Pearson correlation: $R^2 = 0.46$, $P = 0.00$. n = 70).

7.3.3 Seasonality in spawning in *Scarus ferrugineus*

During underwater observations of over 200 hours, 351 spawning ascents were recorded. The highest number per month (80) occurred in March. TTPs visited their territories and spawned daily throughout the year. The spawning rate per minute did not differ among months (Tables 7.2 & 7.3; Fig. 7.7). The number of chasing events min^{-1}, courting min^{-1} and broadside view min^{-1} varied among months and was generally higher between March – April (Table 7.2; Fig. 7.7). Feeding rates of TTPs (bites min^{-1}) were lowest in the cool season and increased towards the summer (Fig. 7.7).

Table 7.2 *Scarus ferrugineus.* Summary of ANOVA results comparing monthly differences in the mean monthly values of spawning related activities. Significant monthly differences are in bold. *df*: degrees of freedom, *F*: f-statistic, *P*= significance.

Category	*df*	*F*	*P*
Spawning	6, 71	1.70	0.14
Courting	6,71	0.05	0.01
Chasing	6,71	0.34	0.06
Broadside view	6,71	0.55	0.04
Feeding	6,71	2.95	0.00

The length of the daily spawning period varied among months. TTPs in general engaged in reproductive activities for longer periods between March – June. The

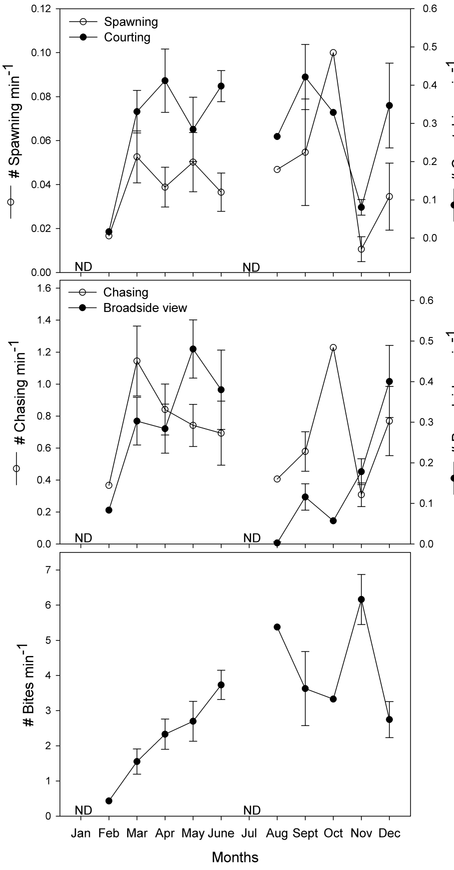

Fig. 7.7 *Scarus ferrugineus*. Monthly trends in mean rates (min^{-1}) of different territorial and spawning related behaviours during the spawning period. ND: no data.

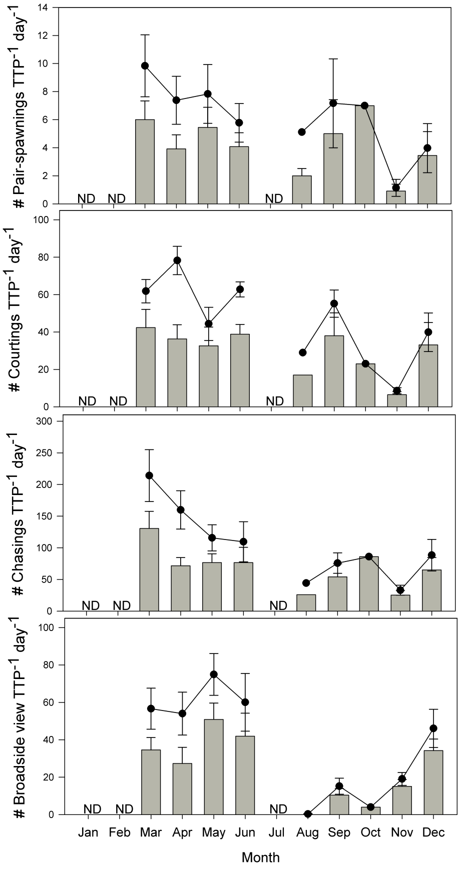

Fig. 7.8 *Scarus ferrugineus*. Monthly trends in the frequency occurrence of spawning and different spawning related behaviours. Bars are the mean values estimated as the product of the mean duration of spawning period and the rate minute^{-1}. Dots and lines are the maximum estimates calculated as the product of the maximum duration of spawning for each month and the rate minute^{-1}. ND: no data.

longest durations were recorded in March (187 minutes) and April (190 minutes) while in the summer months TTPs stayed in their territories for shorter periods (Table 7.3).

Although there was no difference in spawning rate min^{-1}, TTPs tended to engage in more spawning events day^{-1} in the cool season due to the longer duration of the spawning period (Fig. 7.8). A second spawning peak was recorded in September (Fig. 7.8). Monthly trends of the frequency of occurrence TTP^{-1} day^{-1} of the other spawning-related behaviours, such as chasing, broadside view and courting, follow patterns similar to that of spawning (Fig. 7.8). In general, TTPs tended to engage in reproductive activity for longer periods with more intensity during the cool months and in September.

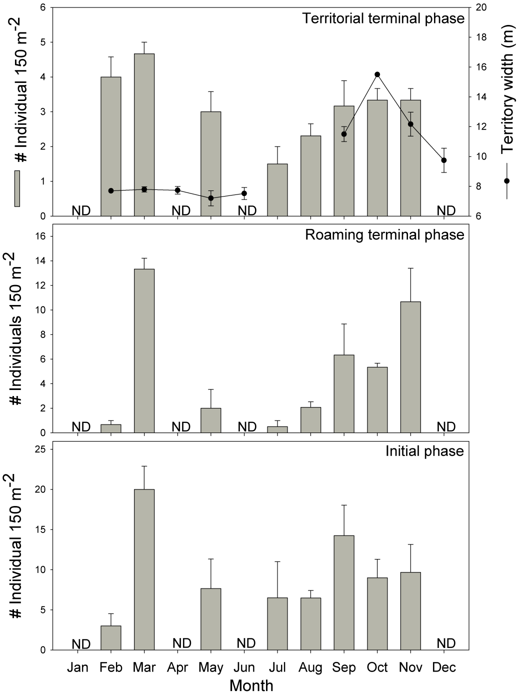

Fig. 7.9 *Scarus ferrugineus*. Monthly means (±SE) of the number of fish counted during spawning periods at the deep fore reef spawning ground. Mean (±SE) number of individual counted during none-spawning periods for March, August, September, October, and November are shown. Also shown is the mean width of the territory occupied by each territorial terminal phase males. ND: no data.

7.3.4 Density of spawners and territory size

During the spawning period, all social categories shoal at the deep fore reef causing a density increase by a factor of 2 – 5 (Chapter 8) compared to the background densities during non-spawning periods. The number of TTPs visiting the deep fore reef varied significantly among months and was the highest during February and March (Fig. 7.9). In addition, the TTPs of *S. ferrugineus* occupied significantly smaller territories during the cooler half of the year compared to the summer months (ANOVA: $F_{6,74} = 12.58$, $P = 0.00$, Fig. 7.9). Abundance of IPs and roaming TPs in the deep fore reef was highest in March, September and November, but the seasonal pattern not as clear as that of the TTPs.

7.3.5 Recruitment

Recruits of *S. ferrugineus* were recorded during most of the year (Fig. 7.10). However, the abundance of the newly settled recruits varied significantly among months with peak numbers of newly settled recruits (0 – 2 cm) during March – June (Table 7.4; Fig. 7.10). A second, smaller, peak in recruitment occurred in November (Fig. 7.10). Recruits primarily settled at the deep fore reef as indicated by the large number of newly settled individuals in this zone (Table 7.4; Fig. 7.10). A few recruits were counted on the shallow fore reef. Newly settled recruits were absent from the reef crest. No recruits of any size were observed on the reef flat.

Table 7.3 *Scarus ferrugineus*. Summary of the length of daily spawning period (minutes) and the spawning rate minute^{-1} for different months of the year.

	Duration of spawning (minutes)					Spawning min^{-1}	
Month	N	Mean	SE	Minimum	Maximum	Mean	SE
February	1	60.00		60.00	60.00	0.017	0.037
March	12	112.50	12.05	65.00	187.00	0.053	0.011
April	12	91.33	10.41	60.00	190.00	0.039	0.011
May	9	105.67	9.75	65.00	156.00	0.050	0.012
June	13	98.46	8.82	60.00	158.00	0.037	0.010
August	6	68.83	8.06	60.00	109.00	0.047	0.037
September	5	85.40	11.88	65.00	131.00	0.055	0.016
October	1	70.00		70.00	70.00	0.100	0.037
November	11	78.82	4.61	62.00	107.00	0.011	0.011
December	9	93.11	7.28	64.00	115.00	0.035	0.012

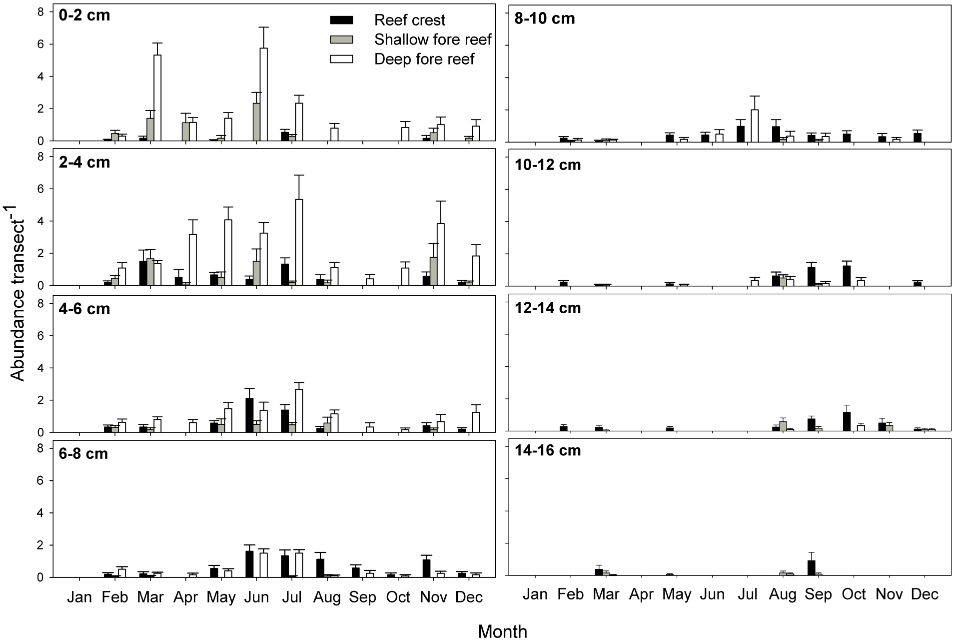

Fig. 7.10 *Scarus ferrugineus*. Monthly means (±SE) of the number of different sized recruits at three reef zones of the fringing reef at Sheikh Said Island.

On the reef crest only larger recruits were recorded, and these appeared several weeks after recruitment peaks in the deep fore reef (Fig. 7.10). The overall temporal and spatial patterns in size distribution indicate that new *S. ferrugineus* recruits first settled at the deep fore reef and as recruits increased in size they progressively moved to the shallower zones, in particular to the reef crest.

Table 7.4 *Scarus ferrugineus*. Summary of GLMM analysis on the number of recruits compared at different months and three reef zones.

Size Class	Intercept		Month		Zones		Zero-Inf-Par	
	df	*P*	*df*	*P*	*df*	*P*	*df*	*P*
1	1(676)	<0.0001	1(676)	<0.0001	1(676)	<0.0001	1(676)	<0.0001
2	1(676)	<0.0001	1(676)	0.6262	1(676)	<0.0001	1(676)	<0.0001
3	1(676)	<0.0001	1(676)	0.9715	1(676)	<0.0001	1(676)	<0.0001
4	1(676)	0.0084	1(676)	0.2684	1(676)	0.0054	1(676)	<0.0001
5	1(676)	0.0191	1(676)	0.0364	1(676)	<0.0001	1(676)	<0.0001
6	1(676)	0.0322	1(676)	<0.0001	1(676)	0.0680	1(676)	<0.0001
7	1(676)	0.0021	1(676)	0.0026	1(676)	0.8149	1(676)	<0.0001
8	1(676)	0.2687	1(676)	0.6759	1(676)	0.2803	1(676)	<0.0001

7.3.6 Diurnal timing of reproduction

S. ferrugineus appears to spawn predominantly during the morning hours. Especially during the cool season most of the spawning episodes were recorded before 10 am (Fig. 7.11). In addition, spawning during the cool season appears to be weakly associated with the time of high tide. In contrast, spawning in June and September appears to be strongly associated with high tide (Table 7.5; Fig. 7.11). During these months spawning and territorial behaviour was not restricted to the morning hours; spawning was recorded up to the early afternoon (1200 hrs till 1400 hrs) if high tide occurred at these times of the day.

Table 7.5 *Scarus ferrugineus*. Summary of the correlation between the time of spawning and the time of high tide at different months.

Month	N	Pearson Correlation coefficient	*P*
March	88	0.49	0.00
April	50	0.55	0.00
May	52	0.73	0.00
June	67	0.86	0.00
September	40	0.76	0.00
October	16	0.42	0.11
November	12	-0.68	0.02
December	33	-0.06	0.74

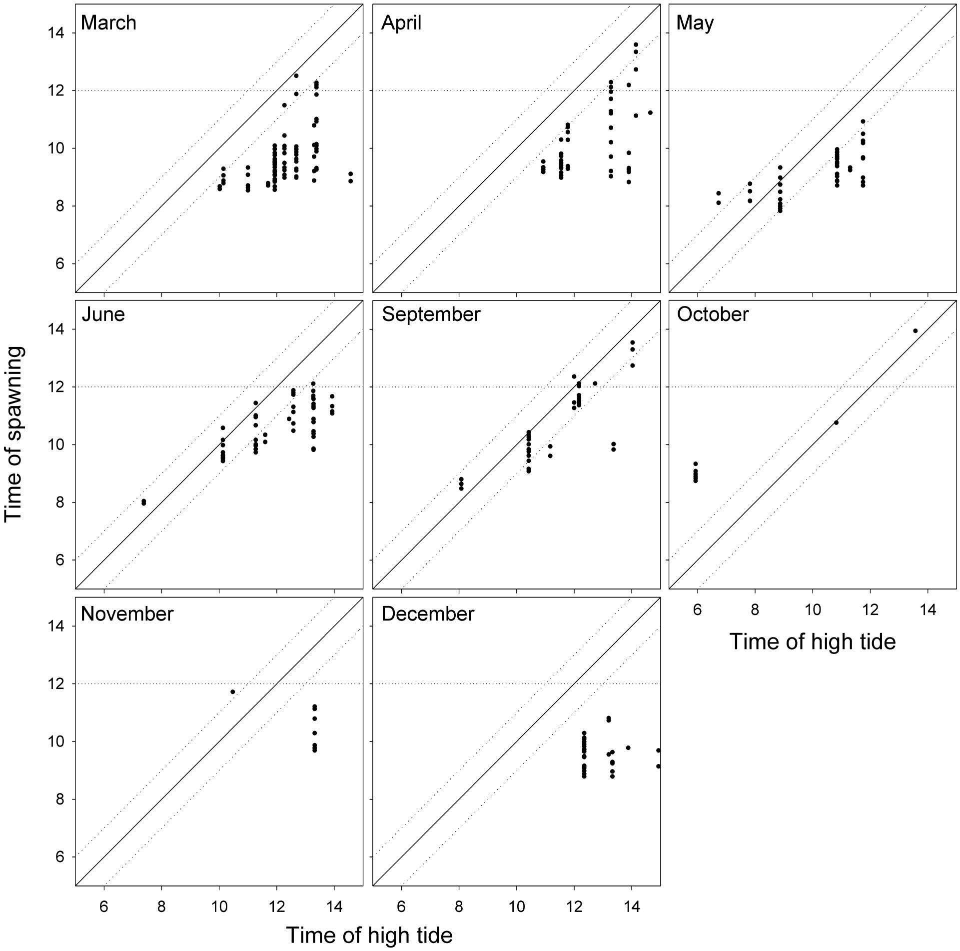

Fig. 7.11 *Scarus ferrugineus*. Diurnal timing of spawning and its relationship with the time of high tide in different months. Dots are the observed spawning times. Solid diagonal line shows perfect match between the time of spawning and high tide. Dotted diagonals are boundaries of spawning occurring within an hour of the high tide. Horizontal dotted line depicts noontime.

7.3.7 Predation on gametes and adults

We recorded frequent attacks on gametes by planktivores. All the attacks we observed were by the Indo-Pacific sergeant major *Abudefduf vaigiensis*. Schools of *A. vaigiensis* actively followed TTPs of *S. ferrugineus* as well as other parrotfishes such as *Chlorurus sordidus* during the spawning period. Once a TTP-IP pair-spawned, individuals of *A. vaigiensis* aggregated in large numbers around the point where the gametes were released showing clear feeding movements of the mouth. They remained feeding on the gametes for some time after termination of the spawning rush. The incidence of gamete predation by *A. vaigiensis* was not uniformly distributed among months (Fig. 7.12). There were close to zero attacks on gametes during the cool season. During the hot season, >50% of all spawning events were predated upon.

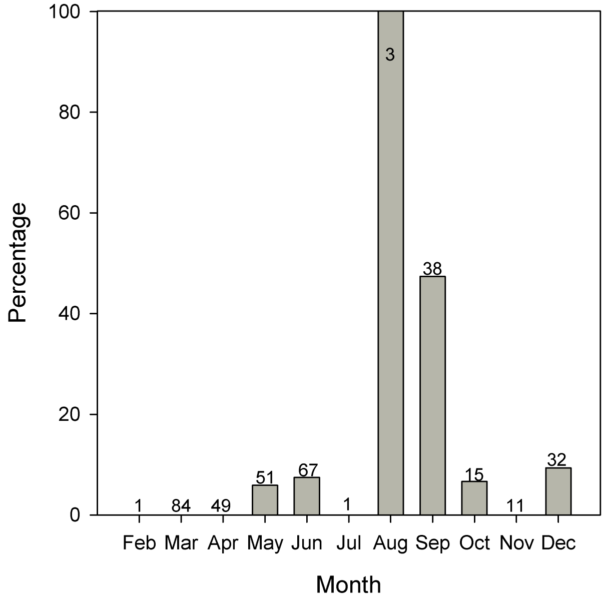

Fig. 7.12 *Scarus ferrugineus*. Percentage of pair-spawning events that were attacked by the planktivore *Abudefduf vaigiensis*.

Several potential predators on adults were recorded at the study site, including the great barracuda (*Sphyraena barracuda*), the bluefin trevally (*Caranx melampygus*), the giant trevally (*C. ignobilis*) and the black tip reef shark (*Carcharhinus melanopterus*). Among these only the giant trevally was recorded attacking the spawning aggregation of *S. ferrugineus*. Nine such predation attempts were recorded, eight of these occurred during September and one in December. Two of these attacks were targeted at a spawning pair just at the moment the spawning rush was about to commence. The pair aborted the spawning move and bolted to the shallow reef. The predator's attack strategy into a pair-spawning involved a dart from the water column followed by a chase. Following each attack the TTPs and IPs cleared the deep fore reef and the entire lek was left deserted until the predator left. Then the TTPs swam back to their territories to resume spawning. Although none of the observed attacks were successful, there was evidence that predation may play an important role in mortality in TTPs. Two TTPs of *S. ferrugineus* and one of *C. sordidus* had their caudal fins completely bitten off during the study. Moreover many of the TTPs had scars on their bodies presumably from failed predation attacks.

7.4 Discussion

7.4.1 Seasonality in spawning

Oocyte development in *S. ferrugineus* is asynchronous as all the developmental stages are present in ovaries throughout the year. Asynchronous oocytes are characteristic of species with a protracted spawning season during which they spawn repeatedly (Wallace & Selman 1981). Our behavioural observations confirm the year round spawning in *S. ferrugineus*. Year round or extended spawning is widely reported in coral reef fishes including parrotfishes (Johannes 1978; Colin & Clavijo 1988; Colin & Bell 1991; van Rooij et al. 1996a). It has been pointed out that despite the extended spawning season in the tropics; fish tend to have peak spawning activity on some parts of the year (Johannes 1978; Colin & Clavijo 1988).

The study population of *S. ferrugineus* showed peak spawning activity during the cool season and to a smaller extent toward the end of the hot season in September. A similar seasonality is reported on a *S. ferrugineus* population from the Saudi Arabian coast (Abdel-Aziz et al. 2012). In *S. ferrugineus* the seasonality in spawning intensity is reflected at two levels: the number of participants and fecundity. More fish participated in spawning activity during the cool season. This is not due to seasonal changes in the overall abundance of the species since our monitoring study has shown that the population remains stable in the course of the study (Afeworki et al. 2013). In addition to their increased participation, a higher proportion of the IP females have mature oocytes during the cool season. This may be because fewer females engage in reproduction during the hot season, which can happen if some females skip spawning for part of the year. In fishes females in low body condition are known to skip a spawning season (Jorgensen et al. 2006; Rideout & Tomkiewicz 2011). Alternatively each female may be spawning at a lower frequency within a season. Studies have shown that females in coral reef fish can spawn every day (Fishelson et al. 1987; van Rooij et al. 1996a; Bushnell et al. 2010). In their detailed study, Bushnell et al. (2010) report lower prevalence rate of repeat spawners (females that spawn in two consecutive days) during the season of low intensity spawning in the surgeonfish *Zebrasoma flavescens*. This suggests that female coral reef fishes could lower the number of days in which they spawn. With the data at hand, it is difficult to determine if the observed pattern in *S. ferrugineus* is a case of skipped season or of skipped days. Clearly more research is needed to understand how IP females decide when to reproduce, at what frequency and what factors are responsible for this.

Stereological analyses indicate that the areal proportion of each oocyte stage estimated from the planar histological cross sections is directly proportional to the volume fraction of the oocytes in the whole gonad (Coward & Bromage 2002b). The volume proportion of oocytes in one developmental stage is in turn an indicator of the fecundity (Emerson et al. 1990). Furthermore, ovary mass is highly correlated with egg production and is useful in predicting egg output during spawning (Clifton 1995; Bushnell et al. 2010). Both ovary mass and the proportion of oocytes in advanced stage of development were lowest during June – July. These two months are probably associated with low fecundity in females. There are reported cases of seasonal variation in fecundity in a coral reef fishes (Clifton 1995; Bushnell et al. 2010), but the proximate causes have not been investigated. Seasonal timing of reproduction in reef fishes has largely been interpreted as an adaptation to increase the survival chances of larvae

(Robertson 1991b). Indeed cases of spawning seasonality in coral reefs have been associated with periods of high pelagic production or with periods characterized by currents that ensure larvae are retained within the natal reef (Russell et al. 1977; 1978; Doherty 1983). The role of pelagic productivity is well known especially in seasonal habitats where a majority of fish species time their reproduction to ensure that the plankthrophic phase of their larvae coincides with the peak pelagic productivity (Qasim 1956; Cushing 1975, 1990). The timing of spawning during calm conditions or when there are gyres near the reef ensures that larvae are retained within the natal reef (Johannes 1978; Lobel 1989; Rodriguez et al. 2001). This is supported by the common observation of high rates of self-recruitment in reef fish populations from these habitats (Jones et al. 1999; Almany et al. 2007).

Neither the peak pelagic productivity nor the calm conditions of the southern Red Sea, coincided with the peak spawning activity in *S. ferrugineus*. This is partly due to the enclosed nature of the Red Sea, which may render pelagic conditions such as currents less important. Indeed, most of the conclusions regarding the role of pelagic conditions on the timing of reef fish spawning are derived from studies conducted on oceanic reefs or exposed continental reefs (Johannes 1978; Doherty 1983; Leis 1986; Rodriguez et al. 2001). Conditions that are important in these localities may not apply to enclosed seas such as the Red Sea. The southern Red Sea is a narrow, enclosed sea with reef habitats abundantly distributed on both the eastern and western sides. Moreover both coasts are littered with numerous islands that have suitable fringing reef habitats. In this area there is very little risk of larvae being carried far away into unsuitable non-reef habitats. Moreover the southern part of the Red Sea maintains a relatively high pelagic productivity thought the year compared to other regional seas (Halim 1984; Longhurst et al. 1995; Veldhuis et al. 1997). These characteristics are likely to render pelagic conditions less influential compared to other oceanic locations.

If pelagic conditions are important in the timing of reproduction then their effects will be expected to be global i.e. different populations will behave similarly and most species in the area should have similar spawning times (Qasim 1956; Russell et al. 1977). Within the Red Sea the spawning seasons of different species vary, implying that the factors responsible for this are local rather than global. Northern populations of many species spawn during the warmer months in summer in the northern Red Sea (Fishelson et al. 1987; Myrberg et al. 1988; Goulet 1995). In contrast, southern species tend to spawn in the cooler parts of the year (Zekeria 2003, this study). In the central Red Sea coast of Saudi Arabia, parrotfishes appear to have a similar spawning season as documented in this study (Gladstone 1996; Abdel-Aziz et al. 2012). In contrast the rabbitfish *Siganus rivulatus* spawns in June, the grouper (*Cephalopholis argus*) spawns from April – August (AL-Masoodi 2012) and the seabream *Rhabdosargus haffara* spawns in December (Abuzinadah 2001). Within the southern Red Sea the spawning times of some reef species differs from that of *S. ferrugineus*. For example, Zekeria (2003) reports peak spawning between April – June in Chaetodonthids and Pomacanthids. *Siganus rivulatus* in the southern Red Sea recruits in December – January (Chapter 2) implying that spawning takes place October – December. These local and interspecific differences suggest that the timing of spawning in these species is not dictated by broad scale pelagic conditions. Instead, the adult biology such as the feeding habits in relation to availability of food and fluctuations in body condition may be responsible for the timing of spawning.

Seasonal changes in biomass, species composition and nutritional composition of algae are known to influence the growth, condition and reproduction of marine herbivores including crustaceans, fish and reptiles (Fishelson et al. 1987; Montgomery et al. 1989; Kennish 1997; Rubenstein & Wikelski 2003). In the Red Sea there are two principal seasons caused by the monsoon (Johannes 1978; Sheppard et al. 1992) and these seasons are associated with changes in benthic algae composition (Ateweberhan et al. 2006a). Briefly described this involves the alternation from high biomass macroalgae dominated season in the cool to one dominated by turf algae in the hot season (Ateweberhan 2004; Afeworki et al. 2011). In addition turf algae during the hot season appear to have higher nutritional quality (Chapter 4).

S. ferrugineus primarily feeds on turf algae with higher preference for turfs that grow on endolithic algae (Afeworki et al. 2011). During May – August the abundance of the preferred resources is high and its inclusion in the diet is high (Ateweberhan et al. 2006a; Afeworki et al. 2011). In addition *S. ferrugineus* feeds at higher rates with a higher daily intake during this period (Chapter 4). This may allow *S. ferrugineus* to simultaneously store energy, invest in gonad development and grow (see Chapter 5 for growth). Positive correlation between investment in gonad development and energy stores during this period suggests that gametogenesis is being fuelled from concurrent food intake. Thus, *S. ferrugineus* appears to act as an "income breeder" during the hot season (sensu Drent & Daan 1980).

During the cool season availability as well as the nutritional quality of the preferred food i.e. turfs growing on endoliths is low (Afeworki et al. 2011) and the intake rate is at its minimum (Chapter 4). The total available energy during the cool season may therefore be limiting. Indeed this season is characterized by low somatic growth (see Chapter 5), low (or declining) body condition and liver mass. Reproductive activity was however maximum during this cool season. A negative correlation between storage and reproduction in the cool season therefore implies that the species is utilizing stored resources to fuel reproduction and is thus behaving as a "capital breeder" (sensu Drent & Daan 1980) during this season.

Capital breeding in marine fishes is usually reported from highly seasonal environments (Jonsson 1997) and is seen as an adaptation to relocate energy from the times of abundance to be used for reproduction at the times that ensure the survival of offspring (Varpe et al. 2009). Capital breeding in tropical and subtropical species has been associated with seasonal changes in abundance of preferred food items (Fishelson et al. 1987; Kennish 1997; Caceres & Ojeda 2000; Rubenstein & Wikelski 2003). However these studies do not explain why capital breeding is needed in these tropical species. Is this an adaptation for spawning at the season of high offspring survival, similar to that reported in cool temperate environments? This is not the case for *S. ferrugineus* (see above).

S. ferrugineus invests more energy and time in reproduction during the cool season to avoid the trade-off between feeding and spawning during the season of peak food availability. Herbivores are known to be energy/nutrient maximizers i.e. they invest most of their time to foraging to maximize their daily intake of nutrients (Nolet & Klaassen 2005; Van Gils et al. 2007). In these animals time spent in none-foraging related activities such as spawning reduces daily intake and their strategy is to minimize these activities (Chapter 4). Coral reef grazers are probably the best examples of energy maximizers as they are known to spend the majority of their daytime hours feeding (Hanley 1984; Montgomery et al. 1989; Bellwood 1995b). In seasonal habitats such as the southern Red Sea, grazers would improve their reproductive output if they minimize time spent on reproduction during the season of peak food abundance. There are a number of indicators that *S. ferrugineus* seems to be maximizing foraging time during the hot season when food is abundant. In this season spawning duration is shorter and the TTPs show significantly lower frequency of spawning related activities such as chasing and courting. As a result, TTPs tend to take more bites per unit time during the spawning period. In summary, *S. ferrugineus* by minimizing the time spent on spawning during the season when its preferred food item is at its peak, maximizes its annual energy intake and hence its reproductive output. Capital breeding in this species thus appears to be a strategy to avoid conflict between feeding and spawning. This strategy will be expected to be common among coral reef grazers inhabiting seasonal habitats.

7.4.2 Diurnal timing of spawning and its seasonality

Most of the spawning activity in *S. ferrugineus* took place during morning hours when the feeding rate is low. In parrotfishes, including *S. ferrugineus* (this study), the time spent on spawning could be 1 – 3 hours (Clavijo 1983; van Rooij et al. 1996a; de Girolamo et al. 1999) and typically the feeding activity during spawning is minimal (Jones 1981; Bruggemann et al. 1994; van Rooij 1996, Chapter 4). In *S. ferrugineus* the cost of spawning amounts to 23% reduction in the daily food intake by a TTP (Chapter 4). Trade-off in time between feeding and spawning is likely to be critical for these grazers who typically spend 80 – 90% of the day time foraging on a poor quality diet (Hanley 1984; Bellwood 1995b; Munoz & Motta 2000). There is clearly a selection pressure for timing the spawning activity outside the peak foraging periods (both diurnally and annually). Robertson (1991b) suggested that the reason why many grazing fishes time their spawning early in the morning is to avoid spawning during the late morning and afternoon hours when they typically feed at maximum rate. A look at the published literature on the timing of spawning in grazers does indicate that these tend to spawn predominantly during morning hours (Clavijo 1983; van Rooij et al. 1996a; Kuwamura et al. 2009). A more telling support for this comes from a study comparing timing in two wrasses (carnivorous) and three acanthurids (herbivores) in American Samoa (Craig 1998). The herbivores spawned during early morning or late afternoon while the carnivorous species spawned throughout the day without clear pattern. At least for herbivorous fishes the diurnal timing of spawning is likely to be determined by the feeding ecology of the adults.

The tendency to spawn in the morning in *S. ferrugineus* is higher in the cool compared to the summer months. During the cooler months spawning does not strictly follow the state of the tide. In contrast in the summer months, spawning follows the state of the tide and may extend into the early afternoon. This could an adaptation to the higher egg predation (see below) in summer. With increasing irradiance and temperature levels in the summer months, the deep fore reef zone may be suitable for feeding during these months. This would make it possible to keep spawning territories in the afternoon hours in the summer months since the TTP could feed and spawn at the same time. The observation that TTPs feed at a higher rate in the deep fore reef during summer supports this hypothesis. Indirect evidence for increased grazing in the deep fore reef in summer includes a lower standing stock of turfs and a higher yield to grazers (Afeworki et al. 2013). In contrast in the cooler months, feeding and hence the yield to grazers is low and as a result turfs attain higher standing stock in the deep fore reef (Afeworki et al. 2013). Although further detailed observation is needed, it appears from the present data that TTP may actually be able to meet their daily energy requirements by being in the deep fore reef in the summer since this zone is more productive during this season.

Another reason why the deep fore reef may be suitable for the TTP during summer is the slightly lower temperature at this zone compared to the reef flat and reef crest. In our previous work we have shown that these large TTPs are close to their upper critical temperature in summer (Afeworki et al. 2013). The dynamics of the fat deposited in the liver and body condition augment this assertion (Fig. 7.5). Indeed fat deposition in the liver rises steeply from April till July in both IPs and TPs (Fig. 7.5). For the IPs fat deposits continue to rise through the summer reaching their peak in October. For the TPs fat deposition stops in the summer and even drops slightly before again starting to grow during the relatively cooler months of October and November. This is a further indication that during the peak of summer the high temperatures may be unsuitable for the large males. All these observations imply that for large TTPs the deep fore reef in summer could be a suitable habitat. This enables them to undertake spawning as well as feeding throughout the early afternoon.

7.4.3 Gamete predators and piscivores

Seasonal variability in egg predation by *Abudefduf vaigiensis* is caused by the seasonality in the reproduction of this species. *A. vaigiensis* is a benthic brooder and starts breeding in the cool season around December and stops by May (Y.A. personal observation). During the breeding season these fish have reduced feeding being entirely engaged in breeding activities (Y.A. personal observation). As a result, the number of attacks on gametes by these species during the cool season is almost zero. Egg predators are thought to have played an important role on the selection of site and time of spawning at the diurnal scale (Choat 2012). Reef fishes spawn on reef edges and at around high tide to facilitate the transport of gametes away from the reef where predation rates are considered to be high (Johannes 1978). For example, Jones (1981) describes how a temperate wrasse spawns in deeper parts of its habitat to avoid egg predators that are abundant on the shallow parts of the reef. For *S. ferrugineus* spawning at high intensity during the cool season has clearly the advantage of avoiding the gamete predators. Whether this has played a role in the timing of spawning in *S. ferrugineus* is difficult to assess at the moment.

Although successful adult predation was not recorded from the field there are several indications that predation may play an important role on TTP mortality. In general direct observation of successful predator attacks on spawning pairs in the field are rare (Sancho 2000; Sancho et al. 2000a). Among the indicators of the prevalence of predation on TTPs include the frequent occurrence of bite marks such as a bitten off caudal fin. Moreover the disappearance of TTP from their territories in less than a year also suggests a high turnover rate. Clearly a carefully planned tagging of TTP and monitoring their movement and residency will reveal the mortality associated with territory keeping. In any case the above observation in combination with our previous result of higher mortality and shorter lifespan in TP than IP (Chapter 5) suggest that piscivory may play an important role on TTP mortality.

7.4.4 Recruitment

The temporal coupling of spawning and recruitment events in *S. ferrugineus* at Sheikh Said Island suggests that either self-recruitment is important or that the *S. ferrugineus* metapopulations around Massawa may have similar spawning seasonality. The time lag between peak spawning and recruitment corresponds with recorded larval durations for parrotfishes (28 – 47 days) (Lou 1993; Schultz & Cowen 1994). This time lag in recruitment is recorded for both the cool season and the September spawning peaks. Marine endemics are usually the numerical/biomass dominant species where they occur (Hourigan & Reese 1987, Chapter 1; Hobbs et al. 2010). Their ability to maintain large populations is related to the high rates of self-recruitment (Eble et al. 2009; Hobbs et al. 2011). *S. ferrugineus* being an endemic species of the Red Sea and the Arabian Sea may have similar traits and the correspondence between spawning and settlement may imply high rates of self-recruitment.

Recruits of *S. ferrugineus* first settle at the deep fore reef and move to the shallow reef zones as they grow. Ontogenetic shift in habitat use among coral reef fishes is pervasive and associated with predation risk and resource availability (Mellin et al. 2007; Ortiz & Tissot 2012). Post-settlement mortality in reef fishes is high and is mediated by the availability of shelter and local abundance of mesopredators (Webster 2002; Holbrook & Schmitt 2003; Almany & Webster 2006; Mumby et al. 2012). At the study site, mesopredators such as the dominant species *Lutjanus ehrenbergii* are common on the shallow reef (Y.A. personal observation). In addition the deeper reef has higher diversity and cover of live corals (Afeworki et al. 2011). This suggests that predation risk for *S. ferrugineus* recruits may be lower at the deep fore reef zone. Alternatively, choice of settlement zone in *S. ferrugineus* may be related to diet and food availability for newly settled individuals (Lecchini & Poignonec 2009). Recruits of parrotfishes are known to feed on crustacean and other animal matter (Bellwood 1988; Chen 2002) and their choice of settlement habitat may indicate higher food abundance (Lecchini & Poignonec 2009). Recruits of parrotfishes include more plant matter in their diet as they grow (Chen 2002). Corresponding with this trend, the larger juveniles of *S. ferrugineus* join the adults in the shallow reef zones where cover, production and quality of turfs are higher (Afeworki et al. 2011).

7.4.5 Conclusion

S. ferrugineus reproduces all year round but with more intensity in the cool season and to a lesser extent in September. Peak recruitment times corresponded with the peak spawning times with a time lag of one to two months. Trends in body condition, liver mass, gonad development and behavioural observations of the intensity of reproduction suggest that *S. ferrugineus* behaves as an income breeder during the hot season and as a capital breeder during the cool season. The choice of the cool season as the time of peak spawning does not appear to be related to offspring survival. Rather it may be related to a trade-off between time spent on feeding and spawning. During the hot season when the preferred food items of *S. ferrugineus* are abundant, *S. ferrugineus* minimizes its reproductive effort to devote most of its day time to foraging. During this season, body reserves are built up that are used during the cool season to fuel reproductive activity. In the cool season despite the shorter days and lower food abundance, *S. ferrugineus* devotes a significant part of the day to spawning related activities. For a herbivorous reef fish like *S. ferrugineus*, the diurnal timing of spawning may be a compromise between the need to spawn at times that decrease larval mortality (high tide) and the need to avoid spawning during the times of peak foraging.

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CHAPTER 8

SEXUAL PATTERNS AND MATING TACTICS OF THE ENDEMIC RED SEA PARROTFISH *SCARUS FERRUGINEUS*

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Abstract Patterns of sex change, the social system and mating tactics of the rusty parrotfish *Scarus ferrugineus* (Forsskål 1775) were studied on a fringing reef in the southern Red Sea, Eritrea. We show that *S. ferrugineus* is a diandric protogynous hermaphrodite with a lek-based mating strategy, using histological sections and field observations of mating behaviour. About 5% of the initial phase population consisted of primary males with solid testis lacking a remnant of ovarian lumen and with a centrally located sperm duct. The majority (86%) of the terminal phase males were sex-changed (secondary males) while 14% are colour changed (primary males). Not all the testis of the secondary males contained ovarian lumen. The areal extent of the lumen varied among individuals from large to no lumen at all, suggesting a process of a progressive occlusion of the lumen. Gonads of females contained presumptive testicular tissue in the periphery of the gonad wall. Large terminal phase males protect a spawning territory at the deep fore reef which they visit daily with high site fidelity. Territories are contiguous and are defended against smaller non-territorial terminal phase males and initial phase males. A maximum of 16 pair-spawnings day^{-1} was recorded for territorial terminal phase males. Initial phase males and small terminal phase males adopt alternative mating tactics including group-spawning and streaking. Territorial terminal phase males occasionally behave opportunistically by streaking into the pair-spawning of a neighbouring territorial terminal phase male. Initial phase males and small terminal phase males had equal success rates in streaking and similar participation rates during group-spawnings. Unlike other labrids, small terminal phase males of *S. ferrugineus* actively participate in reproduction and are functionally equivalent to initial phase males.

To be submitted

8.1 Introduction

A large number of teleosts spread over 27 families are hermaphrodites (De Mitcheson & Liu 2008). A common form is sequential hermaphroditism where an individual first functions as one sex before changing to the other. Sex change from a functional female phase to a functional male phase, is called protogyny (Warner & Robertson 1978; Warner 1984). Males in protogynous species develop either from an undifferentiated juvenile stage (primary males) or from a functional female stage through sex change (secondary males). Species where males develop through both pathways are called diandric while those where only secondary males occur are called monandric (Reinboth 1967, 1980). In labrids, primary and secondary males are relatively easy to distinguish by histological examination since their testes differ in morphology (De Mitcheson & Liu 2008).

Protogyny is closely associated with mating systems that promote the monopolization of mating by large males (Warner 1984). Large males keep temporary (leks) or permanent (harems) spawning territories and pair-spawn with visiting females (Johannes 1978; Colin & Bell 1991; Kuwamura et al. 2009). In diandric species, the initial phase males (female mimics) have heavier testes for their size and engage in streaking and/or group-spawning (Robertson & Choat 1974; Choat & Robertson 1975). In many species small non-territorial terminal phase males may be common and these have been called "bachelors" or "group males" to distinguish them from territorial males (Ogden & Buckman 1973; Ross 1990; van Rooij et al. 1996a). These non-territorial males have either very low reproductive output or are reproductively inactive (Hoffman et al. 1985; van Rooij et al. 1996a). Bachelors are thought to maximize their future reproductive prospects by investing resources to growth and/or survival until they achieve territorial status (Hoffman et al. 1985; van Rooij et al. 1995b; van Rooij & Videler 1997).

Coral reefs harbour a disproportionately large number of protogynous species (Choat & Robertson 1975; De Mitcheson & Liu 2008) and many of these are ecologically and economically important (Sadovy & Domeier 2005). Many "typical" coral reef fish families have protogyous representatives including the Labridae, Serranidae, Gobidae, Pseudochromidae, Pomacentridae (Policansky 1982; Warner 1984; Sadovy & Domeier 2005; De Mitcheson & Liu 2008). The Labridae (wrasses and parrofishes) is one of the largest fish families with over 600 species and a very high diversity in body size, morphology and feeding mechanisms (Westneat & Alfaro 2005; Parenti & Randall 2011). The predominantly hermaphroditic parrotfishes (Choat & Robertson 1975; Robertson & Warner 1978) are among the most common coral reef fishes (Russ 1984a; Afeworki et al. 2013). Parrotfishes have a highly specialized feeding mechanism where they scrape or excavate epilithic algal communities from calcium carbonate substrates using their beak-like fused teeth (Bellwood & Choat 1990). Their feeding action maintains the health of the reef by keeping the algae in a cropped state and by facilitating coral recruitment (Mumby 2006; Mumby et al. 2007; Bonaldo & Bellwood 2009; Bellwood et al. 2012).

In many tropical areas, parrotfishes are targeted by artisanal fishers and their populations have been affected greatly (Hawkins & Roberts 2004b; Clua & Legendre 2008; Lokrantz et al. 2009). Since fishing typically selects large individuals, males suffer higher mortality than females. In situations where size or age of sex change is fixed, overfishing can extirpate males and lead to population declines through sperm limitation (Buxton 1993; Coleman et al. 1996; Hawkins & Roberts 2004a; Molloy et al. 2007). However, mounting evidence suggests that sex change is highly labile (Munday et al. 2006). This implies that species may partly avert sperm limitation by changing sex earlier or at smaller sizes (Platten et al. 2002; Molloy et al. 2007; Gotz et al. 2008; Mariani et al. 2013). To predict how parrotfish will respond to exploitation, basic knowledge of the sex-change patterns and mating tactics is needed

There are 18 recorded species of parrotfishes in the Red Sea (Golani & Bogorodsky 2010). Five of these are endemic to the Red Sea and the Arabian Sea (Randall 1983). Based on field observations, Bebars (1978) reported that all the Red Sea parrotfishes are gonochristic. This is unlikely since many of these species are known to be protogynous from other locations (e.g. *Chlorurus sordidus*, *Scarus frenatus*) (Choat & Robertson 1975). In addition, histological analysis of gonads has confirmed that the endemic *Scarus ferrugineus* is a diandric protogynous species (Abdel-Aziz 2006; Abdel-Aziz et al. 2012). Very little else is known about the social systems and mating tactics of the Red Sea parrotfishes. In particular field studies of the mating behaviour of parrotfishes of the Red Sea are lagging. In this study, we combine histological and behavioural observations to describe the sexual patterns, social structure, and mating tactic of *S. ferrugineus*.

8.2 Materials and Methods

8.2.1 Study site and species

The rusty parrotfish *Scarus ferrugineus* Forsskål 1775 is a diandric protogynous hermaphrodite (Abdel-Aziz et al. 2012) and endemic to the Red Sea and the Arabian Sea (Randall & Ormond 1978; Randall 1983). It is the most common parrotfish in the southern Red Sea (Afeworki et al. 2013). It forages on epilithic algal communities covering dead coral substrates (Afeworki et al. 2011). Terminal phase (TP) individuals are brightly coloured in blue, yellow and purple while initial phase (IP) fish are yellowish brown. Behavioural observations and sample collection for this study were conducted at the fringing reef of Sheikh Said Island (15°35′N; 39°29′E) Massawa, Eritrea. Despite its proximity to the port city of Massawa, the coral reef around the island is in good condition. There is little fishing activity and spear fishing is prohibited here.

Table 8.1 *Scarus ferrugineus.* Mean lengths of the sampled individuals of the different life phase categories and sample sizes used in the study.

Category		Total sample		Sub-sample for histology	
		n	Fork length cm (SE)	n	Fork length cm (SE)
IP	Females	117 (95%)	23.10 (0.18)	57	23.55 (0.21)
	Males	6 (5%)	21.31 (1.07)	4	23.00 (0.55)
TP		102	30.89 (0.38)	44	31.66 (0.41)

8.2.2 Sample collection for histology

Samples for histological examination were collected between 2006 and 2007. For details of the collection method, sample preservation and processing see Chapter 7. Gonads of IP fish were characterized as male or female based on external appearance. After gonads were weighed, half of each was preserved in formalin for histological analysis. Gonad tissue was dehydrated in ethanol, cleared in xylene, and finally was embedded in paraffin. Thin transverse sections were cut on a microtome, mounted on microscopic slides and stained using hematoxylin-eosin. High resolution digital images of the sections were taken by light microscope at ×100 magnification and the analysis was conducted on these. Analysis of oocyte developmental stages and the timing of reproduction are discussed in Chapter 7. Ovary sections were closely examined to check the presence of presumptive testicular tissue, i.e. non-functional sperm germ cells that proliferate during sex change (Smith 1965). Primary and secondary males were distinguished based on the criteria suggested by Reinboth (1962, 1968). Secondary males show evidence of their former female state such as the presence of an ovarian lumen, testicular tissue arranged in lamellar form and a sperm duct that is located peripherally at the testis wall. In contrast, primary males lack the ovarian lumen, have solid testes and the sperm duct is located centrally (Hourigan et al. 1991; De Mitcheson & Liu 2008; Abdel-Aziz et al. 2012).

8.2.3 Field observations of spawning in *Scarus ferrugineus*

To describe the mating tactics of *S. ferrugineus* field observations of territorial males were conducted from August 2007 – June 2008 during the daily spawning period using SCUBA diving. During each dive two observers haphazardly selected two focal territorial TP individuals (TTPs) and recorded the incidence of spawning, courting, and chasing. Replicate observations were conducted on a monthly basis (see Chapter 7 for sampling details). An analysis of the timing of spawning both at the diurnal and annual time scales is given in Chapter 7.

Each spawning event was described by the type of participants as: 1) pair-spawning between one TTP and one IP female, 2) pair-spawning between one IP male and one IP female, 3) pair-spawning between one small TP male and one IP female, and 4) group-spawning defined as those spawning events that involve more than three partners. Each observed group-spawning was further described based on the number of participants and their identity. For each type 1 pair-spawning event, we recorded whether there was streaking or not and whether an IP male, a TP or a TTP did the streaking. Streaking as defined by Warner et al. (1975) is the act of an IP male or a TP rushing to join a type 1 pair-spawning at the moment of gamete release.

TTPs with distinct markings were visited at their spawning territories regularly to determine their site fidelity and residency. For these TTPs the day of first encounter and the exact location of the territory were recorded as well as the last time that this TTP was observed occupying that territory. Furthermore the density of *S. ferrugineus* at the deep fore reef was counted during spawning and non-spawning periods. Comparison of counts conducted during non-spawning and spawning periods indicates whether TTP and IP *S. ferrugineus* maintain permanent territories or use these spawning sites only temporarily.

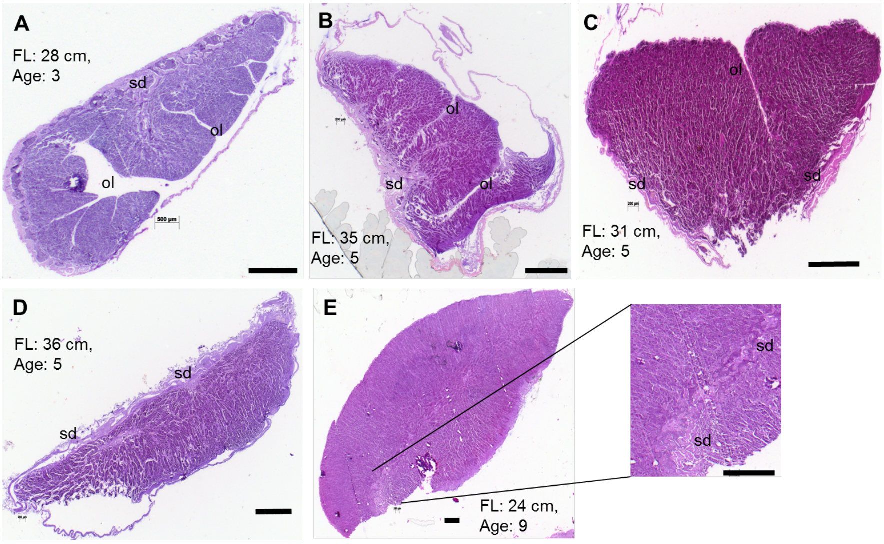

Fig. 8.1 *Scarus ferrugineus.* Transverse sections of testes of secondary males with different ovarian lumen (A) several wide ovarian lumen (B) channel like ovarian lumen (C) a single channel like ovarian lumen (D) lack of an ovarian lumen but with a peripherally located sperm duct (E) initial phase male with a characteristic solid testis and centrally located sperm duct of a primary male. Scale bar at right bottom corner = 1 mm. **sd**: sperm duct, **ol**: ovarian lumen. The fork length (*FL*) and age in years of each individual are indicated. Scale bar at bottom right corner = 1 mm.

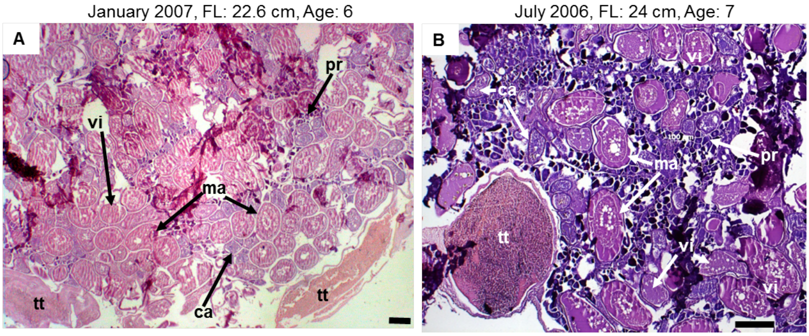

Fig. 8.2 *Scarus ferrugineus.* Transverse sections of ovaries of initial phase females showing presumptive testicular tissue. **pr**: primary growth oocytes, **ca**: cortical alveoli oocytes, **vi**: vitellogenic oocytes, **ma**: mature oocytes, **tt**: testicular tissue. The fork length (*FL*) and age in years of each individual are indicated. Scale bar at bottom right corner = 200 μm.

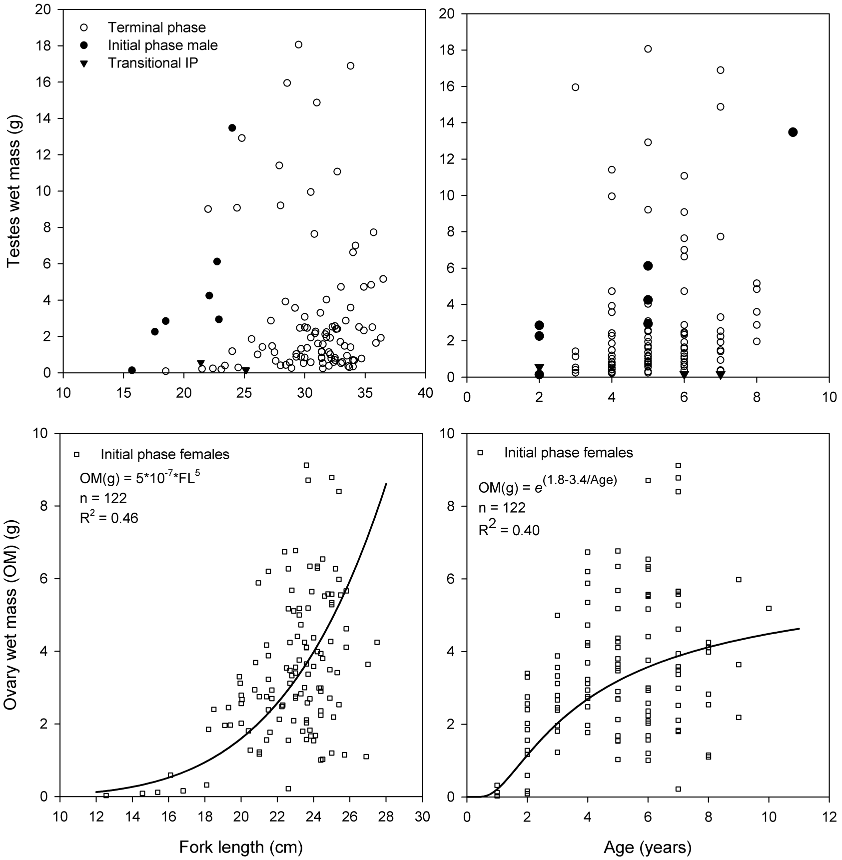

Fig. 8.3 *Scarus ferrugineus.* Wet testes/ovary mass in relation to fork length and age in males and females.

8.3 Results

8.3.1 Histological analysis

Four social and mating categories are identified in *S. ferrugineus*: IP females, IP males, non-territorial TPs (usually small in size), and TTPs. IP males represent about 5% of the total IP population (Table 8.1). Histological examination of the testes of IP males revealed that all of these were primary males (Table 8.2, Fig. 8.1E). Among the TTPs 86% were secondary males (Figs. 8.1A, B, C, D), the remaining 14% were primary males (Fig. 8.1E, Table 8.2). Both IP and TP primary males had a centrally located sperm duct and uniformly solid testis (Fig. 8.1E).

Table 8.2 *Scarus ferrugineus*. Number of histologically examined males belonging to the two male types. Values in brackets are percentages.

Life phase	Primary male	Secondary male	Total
IP	4 (100)	0 (0)	4
TP	6 (13.9)	37 (86.1)	43

About 35% of the secondary males had ovarian lumen. The shape and extent of the ovarian lumen varied with some individuals having large and several such cavities and others having a single slit (Figs. 8.1A, B, C). About 65% of the secondary males lacked ovarian lumen, but had the distinguishing features of a peripherally located sperm duct and lamellar arrangement of tissue (Fig. 8.1D). Testis mass of IP males and small TPs was larger relative to their size compared to the largest TPs (Fig. 8.3). MDS plots based on testis mass and fork length identifies four categories, such that the largest TPs typically have smaller testis for their size compared to both IP males and TPs of intermediate size (Fig. 8.4). Large terminal phase males tended to have smaller testes for their size. The lowest testes mass is associated with the cluster that includes transitional IP, small initial phase males and small TPs. This suggests that these individuals are either immature or in the process of sex-change.

Ovary sections of many IP females contained testicular tissue that was located peripherally on the ovarian wall (Figs. 8.2A, B). Ovary mass was exponentially related to fork length (Fig. 8.3). The relationship between ovary mass and age was not as clear as that between ovary mass and fork length and appeared to be asymptotically related with maximum ovary mass being reached at age 6.

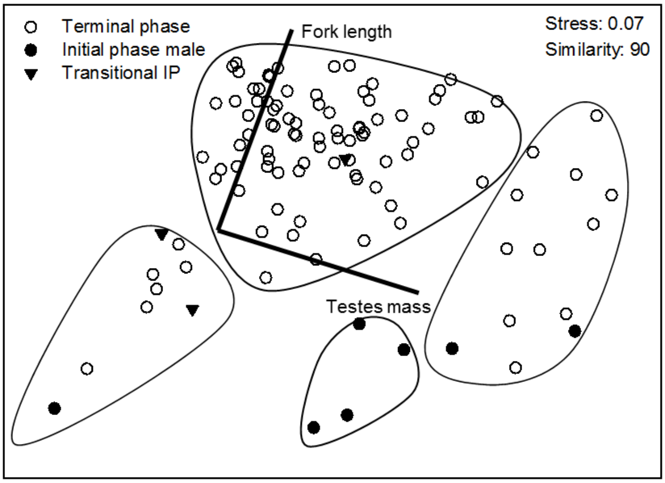

Fig. 8.4 *Scarus ferrugineus*. MDS plot and grouping of different male types based on testes mass and fork length. The loading of testes mass and fork length in the clustering is shown.

8.3.2 Social and mating tactics of *S. ferrugineus*

Our behavioural observations indicate that, all the social categories of *S. ferrugineus* forage in loose groups on the reef crest and parts of the reef flat. At the shallow fore reef they are more dispersed and forage individually. In the deep fore reef (6 – 15 m), foraging activity is minimal and the abundance of this species is low during non-spawning periods (Fig. 8.5). During the spawning periods, all the social categories of *S. ferrugineus* aggregate at the deep fore reef causing the abundance in this zone to more than double (Fig. 8.5). During the spawning periods which occur during the morning hours, TTPs move to the deep fore reef where they patrol a temporary spawning territory. Territories are contiguous and run parallel to the reef. TTPs patrol and defend their territories from neighbouring TTPs, roaming non territorial TPs, and IP males. Intruding IPs (presumably males) and TPs are immediately chased beyond the boundaries of the territory. The frequency of chasing by TTPs on IP males was higher than on small TPs, although the former are rarer in the population (Table 8.5). Outright chasing between neighbouring TTPs was rare (Table 8.5); usually TTPs raised their fins at their common boundary and rarely engaged in aggression.

Table 8.3 *Scarus ferrugineus*. Right side: summary of the prevalence of the different mating tactics during different months. TTP-IP: pair-spawning between TTP and IP, IP-IP: pair-spawning between IP males and IP females, and group spawning: several IPs and TPs spawning together. The number of events recorded and the percentage of occurrence (values in brackets) in each month is given. Left side: the number and the percentage (values in brackets) of pair spawning events (TTP-IP) that were parasitized by streaking by IP males, TPs and neighbouring TTPs.

Month	Spawning			Streaking				
	TTP-IP	IP-IP	Group	IP males	Mixed IP and TP	TP	TTP	Total
February	1 (100.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
March	76 (90.5)	0 (0.0)	8 (9.5)	8 (10.5)	7 (9.2)	19 (25.0)	5 (6.6)	39 (51.3)
April	43 (87.8)	0 (0.0)	6 (12.2)	3 (6.7)	1 (2.2)	4 (8.9)	2 (4.4)	10 (22.2)
May	49 (96.1)	0 (0.0)	2 (3.9)	5 (11.1)	0 (0.0)	0 (0.0)	0 (0.0)	5 (11.1)
June	63 (94.0)	0 (0.0)	4 (6.0)	11 (17.2)	3 (4.7)	5 (7.8)	1 (1.6)	20 (31.3)
July	1 (100.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
August	3 (100.0)	0 (0.0)	0 (0.0)	2 (66.7)	0 (0.0)	1 (33.3)	0 (0.0)	3 (100.0)
September	36 (94.7)	0 (0.0)	2 (5.3)	4 (12.5)	1 (3.1)	3 (9.4)	0 (0.0)	8 (25.0)
October	14 (93.3)	1 (6.7)	0 (0.0)	1 (12.5)	0 (0.0)	4 (50.0)	1 (12.5)	6 (75.0)
November	9 (81.8)	0 (0.0)	2 (18.2)	2 (20.0)	0 (0.0)	2 (20.0)	0 (0.0)	4 (40.0)
December	32 (100.0)	0 (0.0)	0 (0.0)	2 (6.7)	0 (0.0)	1 (3.3)	0 (0.0)	3 (10.0)
Total	327 (92.9)	1 (0.3)	24 (6.8)	38 (12.2)	12 (3.8)	39 (12.5)	9 (2.9)	98 (31.4)

IPs that do not elicit aggressive reaction from the TTPs are assumed to be females. No resident IPs were recorded inside TTP territories. Visiting IP females from outside typically remained there for a while, mainly stayed close to the substrate, and either spawned with the TTP or swam to the next TTP. IP females swim singly or in groups along the territories eliciting courtship behaviour in TTPs. During courtship the TTP swims in circles around the visiting IP. While circling the IP the posture of the TTP is distinctive with the caudal fin compressed and curved downwards. Occasionally the TTP would be bounding with sudden bursts followed by the resumption of the circling movement. This may lead into a TTP-IP spawning rush. A spawning rush occurs when the TTP abruptly moves to the side of the IP and both surge in to the water column at an oblique angle. After spawning, the IP leaves the deep fore reef zone and moves to the foraging grounds of the shallower reef zones.

At the end of the spawning period, which may last from 1 – 3 hours (Chapter 7), TTPs abandon their territories and move to the shallow reef zones to forage with conspecifics. This was ascertained by following TTPs with identifiable natural markings. This is further confirmed by the low density of all phases of *S. ferrugineus* at this reef zone outside of the daily spawning periods (Fig. 8.5). Once at the shallow reef zones, the TTPs that were aggressive to other TPs as well as to IP males down at the spawning site show no agonistic interaction to either IPs or smaller TPs. The above observations essentially suggest that *S. ferrugineus* has a lek based mating system.

Table 8.4 *Scarus ferrugineus*. Residency and site fidelity of territorial terminal phase males (TTPs) at the deep fore reef spawning zone of the fringing reef at Sheikh Said Island, Massawa Eritrea.

TTP	First sighting	Last sighting	Residency (days)	Cause of termination
TTP1	04/09/2007	01/06/2008	267	Disappeared
TTP2	06/09/2007	15/05/2008	249	Disappeared
TTP3	24/09/2007	20/03/2008	176	Disappeared
TTP4	30/11/2007	03/06/2008	183	Disappeared
TTP5	11/12/2007	02/04/2008	111	Disappeared
TTP6	06/03/2008	29/06/2008	113	Study terminated
TTP7	05/04/2008	29/06/2008	84	Study terminated
TTP8	30/05/2008	29/06/2008	29	Study terminated

The different male types recognized here adopted different mating tactics. Large TTPs typically engaged in pair-spawning with IP females. Occasionally TTPs may streak into a pair-spawning of a neighbouring TTP (Table 8.3). In contrast IP males and the smaller TPs engaged in either group-spawning or in streaking. The TTP-IP pair-spawning was the most common mating tactic (Table 8.3) accounting for 92.9% of all the recorded spawning events. Group-spawning (6.8%) was the second common mating tactic was (Table 8.3). We recorded only one incident in which a pair-spawning involved two IPs, one of which is assumed to be an IP male (Table 8.3). The number of fish participating in group-spawning ranged from 3 to 8 with a mode of 6 individuals (Fig. 8.6). IP males and small TPs were equally involved in group-spawning events (Fig. 8.6). About 31.4% of the TTP-IP pair spawning events were parasitized primarily by IP male (12%) and small TPs (12%). A smaller percentage (3%) of the streaking was by TTPs who acted opportunistically to parasitize the pair-spawning of a neighbouring TTP (Table 8.3). More than one individual was involved in 3.8% of the streaking events.

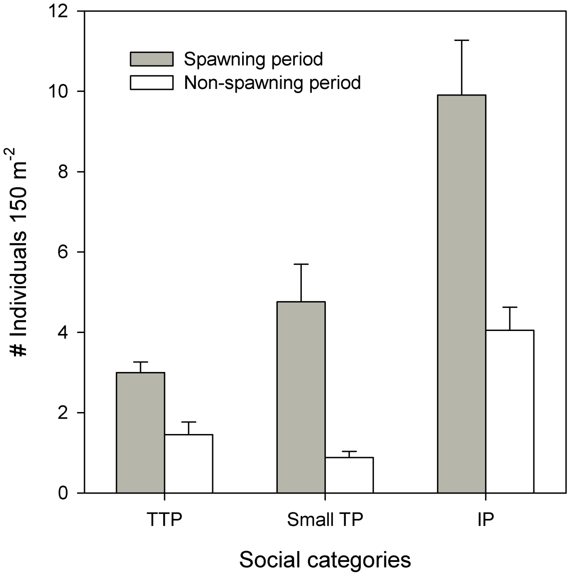

Fig. 8.5 *Scarus ferrugineus.* Mean (±SE) of abundance of the different social categories at the deep fore reef zone during spawning and non-spawning periods.

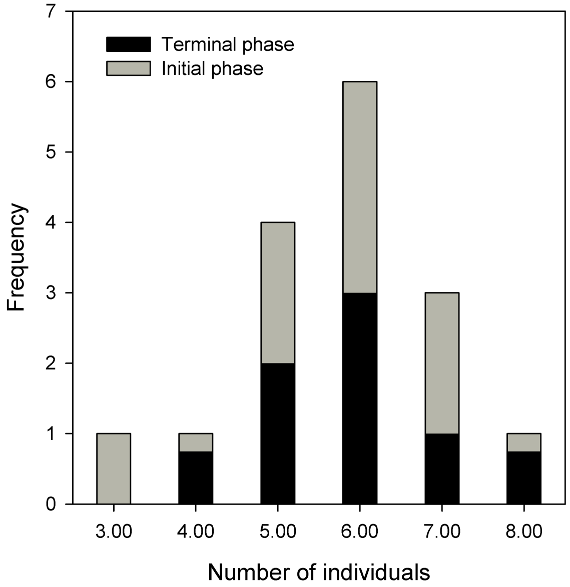

Fig. 8.6 *Scarus ferrugineus.* Frequency distribution of group sizes during group-spawning events. The mean number of initial phase and terminal phase involved in each category are indicated.

8.4 Discussion

8.4.1 Protogyny in *Scarus ferrugineus*

Ormond and Randall (1978) characterized *S. ferrugineus* as a monandric protogynous hermaphrodite with pair-spawning habits based on a sample size of 24 IP fish and on external morphological observations. A larger sample and detailed histological analysis, by Abdel-Aziz et al. (2012) showed that *S. ferrugineus* is a diandric species. Our own data support this. The IP males composed 5% of the IP population a value similar to that reported for a Saudi Arabia population (Abdel-Aziz et al. 2012). In both cases all the examined IP males are primary males with solid testes and a centrally located sperm duct. In addition *S. ferrugineus* has a female biased sex ratio although the largest size classes are dominated by males (Chapter 6). Both these traits are associated with protogyny (Sadovy & Shapiro 1987). While investigating the growth of *S. ferrugineus* (Chapter 5) using tagging techniques, three individuals changed colour to become terminal phase males. The latter provides a more direct evidence for sex change in this species.

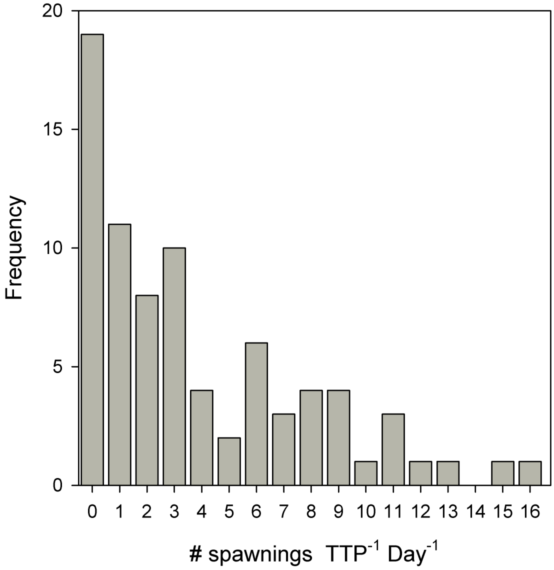

Fig. 8.7 *Scarus ferrugineus*. Frequency distribution of the number of pair-spawning events day^{-1} that territorial terminal phase males (TTP) engage in during the daily spawning period.

Most of the TP in *S. ferrugineus* were secondary males derived from females with only 14% being primary males. Similar values were reported for the Saudi Arabian population (Abdel-Aziz et al. 2012). A review of published data on diandric parrotfishes shows that the proportion of primary and secondary males in the TP mirrors the proportion of males and females in the IP (Fig. 8.8). This relationship which was pointed out early by Choat and Robertson (1975), implies that the propensity to become a TP either by colour or by sex and colour change is similar for IP males and IP females. It follows from this that being an IP male is not a route to

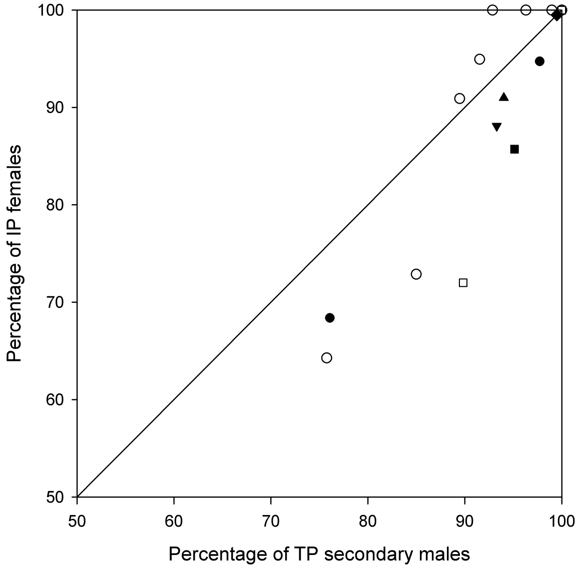

Fig. 8.8 Diandric protogynous parrotfishes (family Labridae). Relationship between the percentage of IP females and secondary males in the terminal phase males. Line depicts equal proportionality. Sources for the scatter points are: (○): Choat & Robertson (1975), (●): Robertson & Warner (1978), (□): Robertson et al. (1982), (▲): McILwain & Taylor (2009), (▼): Abdel-Aziz et al. (2012), (⧫): Kusen & Nakazono (1991), (■): this study.

being a dominant male through colour change; rather it is a distinct breeding tactic adopted by a subset of the IP population.

Among parrotfishes and wrasses the presence of ovarian lumen in secondary males appears to be common and is useful in distinguishing secondary males from primary males (De Mitcheson & Liu 2008). Previously all secondary males of *S. ferrugineus* were reported to have ovarian lumen (Abdel-Aziz et al. 2012). Our results differ from this in that some of the secondary males of *S. ferrugineus* had ovarian lumen while others lacked it. When the lumen was present its shape and extent varied from extensive structures to diminished slits. This variation suggests stages of a process where the ovarian lumen progressively gets occluded until it eventually disappears. Such occlusion of the ovarian lumen may be possible if testicular tissue progressively fills up lumen over time. A similar process in secondary males including parrotfishes has been described before (Shapiro 1981; De Mitcheson & Liu 2008). What causes the occlusion in *S. ferrugineus* is unknown but may be associated with the length of the time period since sex change.

Abdel-Aziz et al. (2012) did not find testicular tissue in the ovary of IP female of *S. ferrugineus* from Saudi Arabia. They indicate that testicular tissue only appears during sex change. Here, small peripherally located testicular tissue was clearly present in many of the ovary sections that we examined. It is important to note that these sections were from IP females with functional ovaries containing mature and vitellogenic oocytes and not from degenerating ovaries with atretic oocytes. It is unlikely, though not impossible, that the differences in gonad anatomy between the samples from either side of the Red Sea may be inter-population differences. A more likely explanation is that the testicular tissue structures might have been overlooked in the Saudi Arabian samples. The distribution of this testicular tissue is known to be localized, for example in Serranids where the "presumptive testicular tissue" is located around the midsection of the ovary (Sadovy & Domeier 2005). Because of its restricted distribution, not all histological sections will include the testicular tissue. This is consistent with our observation in which we found these structures in some but not in all gonad sections examined. As suggested by Sadovy & Domeier (2005), examining sections from different points along the length of the gonad may resolve the problem.

8.4.2 Mating tactics

Different mating tactics have been reported in parrotfishes including group-spawning, harems and lekking (Colin 1978; Robertson & Warner 1978; Clavijo 1983; van Rooij et al. 1996a; Munoz & Warner 2003a). Our behavioural and abundance data show that *S. ferrugineus* is a lekking species that aggregates at the deep fore reef for spawning purposes. All social categories of *S. ferrugineus* converge at the deep fore reef during spawning periods as indicated by increased abundance during the periods when reproduction takes place. Most of the other parrotfishes at the study site such as *C. sordidus*, *Hipposcarus harid* and *Scarus collana* aggregated at the deep fore reef during similar times as *S. ferrugineus* and their territories overlapped (Y.A. pers observation). There is a similar tendency in other lekking species (e.g. *Scarus vetula*) for their abundance to increase in the deeper portions during spawning (Clavijo 1983; Colin 2012; de Mitcheson & Colin 2012). Domeier (1997) identified two kinds of spawning aggregations in reef fishes "transient" and "resident" aggregations. Resident spawning aggregations are characterized by small distance migrations generally occurring within the home ranges of the species. They tend to occur frequently and last a few hours daily. Species forming resident aggregations have small to medium body size and tend to be herbivorous (Domeier & Colin 1997; Choat 2012). The aggregations of *S. ferrugineus* and the other scarids at the study site fit the definition of "resident spawning aggregations" . Resident aggregations usually take place on well flushed locations such as the reef edge or deeper portions of the reef (Choat 2012; Colin 2012). Choice of these locations is thought to be an adaptation to promote the dispersal of gametes away from the reef where predation by planktivores is high (Choat 2012).

The streaking frequency in *S. ferrugineus* is in the high range of those reported for scarids (Robertson & Warner 1978; Clavijo 1983; de Girolamo et al. 1999; Kuwamura et al. 2009). This partly reflects the high density of the species at the study site (Afeworki et al. 2013). In large populations the ability for large males to monopolize spawning becomes costly and this leads to more success for the alternative male mating tactics adopted by IP males (Warner & Hoffman 1980a; Warner & Hoffman 1980b). In general, the incidence of group-spawning and streaking tends to be high in larger populations (Kuwamura et al. 2009). Moreover habitat characteristics such as availability of hiding places for IP males and small TPs may influence the streaking frequency with more complex habitats favouring streaking (Robertson & Warner 1978; Warner & Robertson 1978; van Rooij et al. 1996b). TTPs of *S. ferrugineus* keep their territories at the transition zone between the reef and the sand plain of the deep fore reef where hiding places for the streakers is low. However, the high water turbidity at our study site may play a similar role as the availability of hiding places. This high turbidity plus the high density of the species at the study site may contribute to the high prevalence of streaking in this population.

Some TTPs behaved opportunistically and streaked in to a pair-spawning by a neighbouring TTP. This behaviour has been reported in other labrids (Warner & Robertson 1978; Bell 1983). A possible explanation for this opportunistic behaviour in territorial males is provided by Suzuki et al. (2010) who showed that territorial males in the wrass *Halichoeres trimaculatus* participate in group-spawning when their success rate in their own territories is low. With the data at hand it is not possible to identify what factors are associated with this behaviour in *S. ferrugineus*.

The mating tactic of IP males is well known and involves both group-spawning and streaking (Warner et al. 1975; Warner & Robertson 1978; Warner & Hoffman 1980b). Small non-territorial TPs (<30 cm fork length) in our population are abundant and their size range overlaps with that of the IPs. These small TPs are essentially a third social category of males and our behavioural observations indicate that they adopt the same alternative mating tactics of streaking and group-spawning as the IP males. Kuwamura et al. (2009) made similar observations for *Scarus rivulatus* on a Japanese fringing reef, where small TPs actively participated in group-spawning. Previously, small non-territorial TPs were called "bachelors" and were considered reproductively inactive (Robertson & Warner 1978; Cardwell & Liley 1991; van Rooij et al. 1996a). The existence of "bachelors" was explained as a strategy to channel resources to growth in order to become large enough to occupy a territory of their own (Hoffman et al. 1985; van Rooij et al. 1995b). This is valid if reproduction affects growth or mortality of the small TPs (Iwasa 1991). Our work shows that transitional individuals and small TPs have the fastest growth in *S. ferrugineus* (Chapter 5) suggesting that their reproductive activity does not reduce their growth. This is plausible since, small TP do not spend energy for territory defence. Their primary reproductive cost is sperm production and this may not significantly affect growth. Indeed unlike egg production, sperm production only constitutes a small percentage of the basal metabolic cost of animals (Hayward & Gillooly 2011).

Table 8.5 *Scarus ferrugineus*. Summary of the incidence of chasing by territorial terminal phase (TTP) males on intruding initial phase males (IP males), small TPs, and neighbouring TTPs.

Target	Estimated percentage**	Number of chases (percentage)
Small TP	15	2395 (35.5)
IP	3.5	3231 (47.9)
Unclear target*		736 (10.1)
TTP	15	386 (5.7)
Total		6748 (100)

*The target of these chases were not recorded

**The percentage occurrence of each category in the population was estimated based on the percentage of IP (70%) and TP (30%) (Chapter 6), and the percentage of IP males within the IP (i.e. 5%). TP <30 cm make up 50% of the TP and are here considered non-territorial.

In our *S. ferrugineus* population, IP males and small TPs are similar in three essential ways. Both tended to have larger testis for their size, a trait that is inherently associated with breeding tactics that have high sperm competition such as group-spawning and streaking (Choat

& Robertson 1975; Marconato & Shapiro 1996; Taborsky 1998). Their participation in streaking and group-spawning events was equivalent. Interestingly, the rate of chasing by TTPs was much higher for the IP males despite their lower frequency in the population (Table 8.5). As suggested by Warner & Robertson (1978), behavioural or chemical cues may give away the identity of the IP male resulting in an outright chase. These observations suggest that the "female looks" of the IP males of *S. ferrugineus* do not bring better success in streaking or group-spawning or in intruding into a TTP territory. This further suggests that, at least in *S. ferrugineus*, IP males and small TP males are functionally equivalent. However, it is possible that other advantages, such as reduced predation rate due to their drab coloration, may be higher for IP males. Clearly further research is needed to understand the adaptive value of being an IP male compared to a small TP individual. Early sex-change and non-territorial status of small TPs is not necessarily associated with a reproductive hiatus as formerly reported. These small TP males may actively engage in reproduction and still manage to grow fast to reach the large sizes that enables them to compete for a breeding territory later.

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Chapter 9

General discussion

The southern Red Sea is characterised by distinct seasonality (outlined in Chapter 1) and offers a natural setting to investigate how a coral reef grazer will respond to significant shifts in availability of potential food sources. In addition this area features among the most extreme summer temperatures experienced by coral reefs. The aim of this thesis was to investigate the effect of these two conditions i.e. seasonality and extreme summer temperatures on a large-bodied herbivorous reef fish *Scarus ferrugineus*. The study reveals dramatic seasonal effects on feeding, growth and reproduction. Moreover extreme summer temperatures are responsible for shifts in habitat use, lowered condition and feeding in the largest individuals of *S. ferrugineus*.

9.1 Seasonality

9.1.1 Changing food availability

Algae are a major component of the benthic biota of coral reefs (Adey 1998). In the southern Red Sea area cover of algae ranges from 20 to 60% of the coral reef (Zekeria & Videler 2000; Afeworki et al. 2011). Erect foliose and canopy forming macroalgae are mainly restricted to the reef flat. The reef crest and shallow and deep fore reef are dominated by live corals, turf algae and crustose corallines (Ateweberhan et al. 2006a; Afeworki et al. 2011). Phenology of algae in this area follows a highly predicable seasonal pattern with the cool season supporting a large biomass of macroalgae and crustose corallines in the shallow reef zones (Ateweberhan et al. 2006a; Afeworki et al. 2011). These die and give way to turf algae during the hot summer months. The availability and nutritional quality of turf algae is highest in the hot season (Afeworki et al. 2013, Chapter 4).

How this spatial and temporal variation in resource availability affects coral reef grazers was investigated by studying the habitat use patterns among the common roving herbivorous fishes (Chapter 2). Habitat use by roving herbivores (habitat is defined here as the reef zone where a species forages) reflects their feeding preferences. For most of the year macroalgivores such as *Siganus rivulatus* are the most abundant grazers on the reef flat. While species, that largely feed on turf and associated biota, such as *S. ferrugineus*, achieve their peak density on the reef crest where the cover of this resource is the highest. This pattern changes during the hot season when the distinction in habitat use among the species disappears. This is partly due to the homogenization of the habitats, associated with the loss of macroalgae from the reef flat during summer.

Seasonal estimates of turf biomass and yield to grazers in different zones indicate that during summer the grazing impact declines on the reef flat while it increases in the deeper reef zones. In addition, the abundance of grazers on the reef flat decreases slightly during the hot season. The shift in grazing intensity from the shallow to the deeper parts of the reef during summer appears to be related to the extremely high summer temperatures on the reef flat.

9.1.2 Grazing by *Scarus ferrugineus*

S. ferrugineus is the biomass dominant grazer at the study site (Chapter 2). It mainly forages on the reef crest and the shallow fore reef. Feeding preferences of *S. ferrugineus* – estimated from field records of available resources and bites taken – change seasonally (Chapter 3). The species is highly selective and primarily takes bites from dead coral substrates covered by turf algae. Turfs growing on endolithic algae are preferred over those growing on crustose corallines. In the cool season, the cover of turfs growing on endolithic algae diminishes while those growing on crustose corallines increases. As a result, *S. ferrugineus* augments its feeding by taking more bites on turfs growing on crustose corallines. Other potential food sources that become abundant during the cool season like macroalgae and crustose corallines are not utilized. Food selection in *S. ferrugineus* varies diurnally, where individuals forage on less preferred food items and substrates during the morning. During the rest of the day individuals typically forage on open horizontal surfaces covered by the preferred food items. In general, *S. ferrugineus* appears to compensate for the lowered availability of turfs growing on endolithic algae by including more turfs growing on crustose corallines. However this flexibility is limited and does not extend to other potential food sources such as macroalgae and crustose corallines.

Like other parrotfishes, *S. ferrugineus* prefers to graze on the relatively smoother surfaces of dead corals mostly originating from massive species. *S. ferrugineus* tends to avoid rugged dead coral surfaces originating from branching corals or coral rubble. In the event of massive coral die-off, the efficacy of parrotfishes to keep the algae in a cropped state will thus also depend on the relative composition of the different coral morphologies in the habitat (Bennett et al. 2010). Feeding rate in fish generally increases with food availability and temperature. *S. ferrugineus* shows seasonality in intake rate that corresponds with the variation in temperature and availability of its preferred food resource (Chapter 4). *S. ferrugineus* takes more bites per day in the hot than in the cool season. As a result the total daily food intake (g AFDM day^{-1}) is lowest in the cool season and highest during the May – June period (Chapter 4). *S. ferrugineus* is nutritionally better off during hot season compared to the cool season. As is shown below, this seasonal variation in intake influences growth and reproduction.

9.1.3 Growth, condition and reproduction

The effect of seasonally varying food intake was investigated by recording growth rate using mark-recapture techniques (Chapter 4) and by studying physiological condition and reproductive output during different seasons (Chapter 6). Monthly samples of Initial Phase (IP) and Terminal Phase (TP) fish were collected to assess body condition, liver mass and the weight development of the gonads. Seasonality in reproduction was further investigated by field ob-

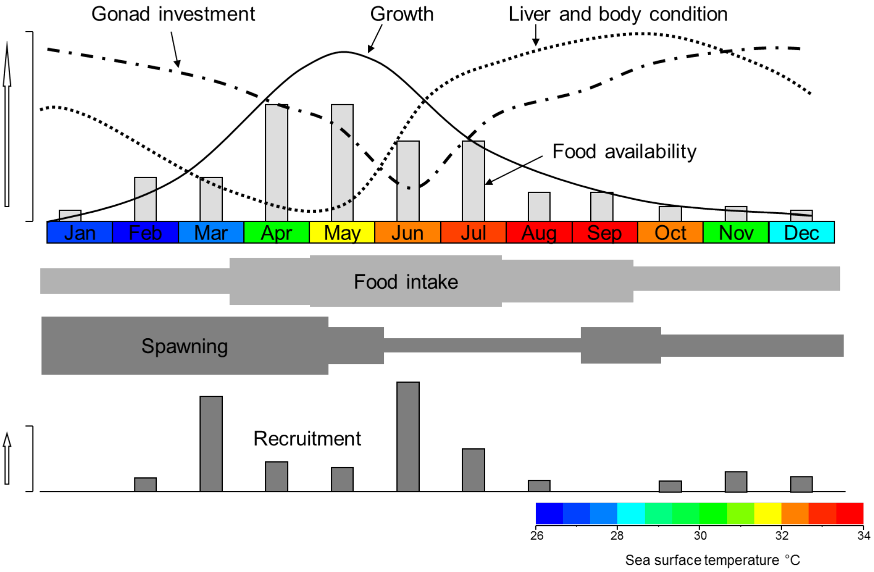

Fig. 9.1 A year in the life of *S. ferrugineus*. A schematic representation of the phenology of *S. ferrugineus* on the southern Red Sea reefs.

servations of daily spawning behaviour and monthly recruitment counts. Both growth and body condition correlate with intake rate and the availability of the primary food resource (Fig. 9.1). Growth is fastest during the warmer parts of the year reaching a peak around June. During the cool season growth ceases. Moreover *S. ferrugineus* has the highest liver and body condition in the warmer parts of the year with the peak state during the June – October period (Fig. 9.1). Liver mass and body condition are either low or are declining during the cool season (Fig. 9.1). Throughout the year, *S. ferrugineus* engages daily in spawning activity, but spawning intensity varies with season. All spawning related activities (i.e. incidence of spawning, number of fish participating in spawning, and the number of spawning events) are highest during the cool season. In addition, testis weight, gonad weight and the maturation stage of oocytes are highest during the cool season (Fig. 9.1).

During the cool season reproduction peaks while body energy reserves decline (Fig. 9.1). This demonstrates that this species is utilizing stored energy to fuel its reproduction during this season and is thus behaving like a capital breeder. Capital breeding strategy is typical of highly seasonal habitats of temperate zones. In temperate habitats capital breeding is used to time reproduction during the period when offspring survival is maximal. In *S. ferrugineus* capital breeding and the more intense spawning during the cool season does not correspond with pelagic conditions that promote larval survival. Instead *S. ferrugineus* appears to adopt capital breeding to minimize the conflict between feeding and spawning.

Like most coral reef grazers, *S. ferrugineus* is an energy maximizer who devotes most of its daytime hours to foraging. Any activity that minimizes the time spent foraging is likely to reduce its fitness. Reproductive activity in *S. ferrugineus* and other parrotfishes takes a significant part of the day time which may lead to significant reductions in food intake. For instance territorial males of *S. ferrugineus* lose 23% of the daily food intake as a result of reproductive activities compared to males that are non-territorial. *S. ferrugineus* shows several behaviours that seem to reduce the conflict between feeding and spawning during the warmer parts of the year when its primary food is most abundant. Males engage in spawning activities for a shorter duration in the hot season. Also the frequency of chasing, courting, and spawning are lower during the hot season. Since the day light hours are longer in this season, the combined effect is that the overall time spent foraging is much higher in the hot than in the cool season. This allows the territorial TP to realise higher a food intake while still maintaining spawning activity. The possibility of a trade-off between foraging and spawning in coral reef grazers and its role in influencing the timing of reproduction deserves to be researched in more detail.

9.2 Extreme summer temperature

Over the past few decades global sea surface temperatures (SST) have increased due to global warming. In the Red Sea, the corresponding SST increase occurred rapidly in the mid 1990s (Raitsos et al. 2011). It occurred in the form of a step change that shifted the sea into a warmer state (Chapter 1). Our records of *in situ* SST from the study site are from 1997 – 2006, hence shortly after this jump in temperature (Guillaume et al. 2000; Ateweberhan et al. 2006a). These records show that the summer SSTs regularly exceed 34°C, while temperatures higher than 32°C last for more than 3 months. The ecological phenomena reported in this study may thus represent responses to a changing environment.

9.2.1 Effects on habitat use

There were several indications that extreme summer temperatures may be limiting to coral reef fish populations at the study site. One of these is the shift in grazing intensity from the shallow to the deeper parts of the reef (Chapter 2). Temperature mediated mobility downshore is common in temperate habitats and involves migration to the deep during the winter and upshore during the warmer parts of the year. Along the shores of the southern Red Sea an opposite trend appears to occur, probably due to the extremely high temperatures in summer (Chapter 2).

If SST rises as is predicted by global warming models, the shallow reef flat habitats of the southern Red Sea will become even more inhospitable. The role of grazers in controlling the macroalgae of this reef zone may be diminished. Unlike fish, macroalgae are able to survive these conditions either as spores or as dormant primary laterals (Ateweberhan et al. 2005a; 2005b). This suggests that extreme temperatures may provide reef flat algae a refuge from grazing during part of the year. This can potentially lead to recruitment success and/or lowered grazing-induced loss of primary laterals. Better survival of recruits and primary laterals of macroalgae during summer (Ateweberhan et al. 2005a) suggests that such a process is already underway.

9.2.2 Effects on foraging and body condition

Extreme high summer temperatures appear to limit grazing rate in the larger sizes of *S. ferrugineus* since their feeding rate tapers off at high temperatures while that of the smaller IP individuals increases linearly with temperature. Furthermore, the accumulation of liver fat stops and slightly drops during the hottest months (August – September) in TP males (Chapter 7). The large TPs may be unable to compensate for the increased metabolism during this period, resulting in the slight decline in liver fat and stoppage of fat accumulation. With a slight drop in temperature in October and November, TPs once again deposit fat in the liver. In contrast, liver weight of the smaller IPs increases steadily throughout summer corresponding to their high feeding rates in the hot season. These observations suggest that the larger TP males are close to their upper critical temperature and are therefore constrained by limited metabolic scope during summer.

9.2.3 Effects on life history

Our analysis of demography and life history of males and females using age-length data (Chapter 5) shows that TPs of *S. ferrugineus* suffer higher mortality than females and as a result have shorter life span. Predation and the extreme temperature of the habitat are the likely agents that might have led to this difference. Males are more vulnerable to predation because of their bright coloration and their spawning behaviour (Clifton & Robertson 1993; Sancho et al. 2000a). At the study site several predation attempts on spawning pairs and bite marks on territorial males, possibly from failed predation attempts, were observed. These indicate that selective predation may partly explain the higher mortality rate of males.

High temperature of the site is the other likely cause of the shorter life span (higher mortality) of the males. In ectotherms in general, high temperatures lead to higher mortality rates (Atkinson 1994) and this effect is expected to be more pronounced in larger individuals (Pörtner & Knust 2007). Size selective effect of high temperature on aquatic organisms is well known and typically large individuals reach critical temperatures earlier (at lower temperatures) than smaller individuals (Hernandez et al. 2002; Pörtner & Knust 2007; Pörtner et al. 2008). Temperature effects on the demography of parrotfish populations in the southern Red Sea have previously been demonstrated by comparing populations from the hot Massawa bay with those of the slightly cooler fringing reefs of Assab (Afeworki 2003). Apparently the higher temperature of Massawa has resulted in populations that have significantly smaller asymptotic sizes and higher mortalities. This is consistent with the well established effect of temperature on the demography of ectotherms.

Sex difference in longevity seems to have set a threshold age beyond which the expected reproductive success as a sex changed male is lower than when staying female. Females can postpone sex change for lack of suitable social or environmental conditions. Indeed, sex change is highly flexible and is triggered when the suitable social and environmental cues are available (Shapiro & Lubbock 1980; Warner & Swearer 1991; Munday et al. 2006). It is therefore plausible that a female can remain unchanged beyond this threshold age if the suitable cues are not presented. Our mechanistic model predicts that a female that has not changed sex until 5 – 6 year old, will maximize its lifetime reproductive output by not changing sex. Higher mortality in males of *S. ferrugineus* sets this upper threshold and explains the presence of older none-sex-changing females. Many protogynous fish species have similar demography as that of *S. ferrugineus* which indicates that mortality difference between the sexes may be a common feature of protogyny.

9.3 Conclusion

S. ferrugineus, like most other parrotfishes, is adapted to a diet based on epilithic algal community (EAC). Seasonal changes that lower the availability of this food source affect the growth and reproduction of this species. Large scale spatial and temporal changes in benthic communities especially those that tend to increase macroalgae at the expense of the EAC, will affect the growth and reproduction of parrotfishes. In contrast macroalgivores such as *S. rivulatus* may benefit from this. Major changes in benthic algal communities are therefore likely to influence population processes and ultimately alter the species composition of grazers. The above also suggests negative feedback mechanism between macroalgae and parrotfish population processes. It is therefore important to investigate how population processes in grazers are influenced by these environmental changes and if there are negative or positive feedback mechanisms involved.

Coral reef fish have two key life history stages, the larval and the adult phases. It is understandable that processes that affect either of these two stages will determine population size (Jones 1991; Jones & McCormick 2002). Nevertheless, coral reef researchers have paid more emphasis to the larval phase, as this stage is largely believed to be limiting to coral reef fish communities (Doherty & Williams 1988; Doherty 2002). This study showed that somatic growth and reproduction in *S. ferrugineus* was highly seasonal being largely determined by resource availability. Recruitment followed a predictable pattern with peak recruitment occurring a month or two after spawning. Seasonality in spawning did not correlate with pelagic conditions that are expected to promote larval survival. It appears that conditions in the adult population in particular the conflict between foraging and spawning is largely responsible for the overall seasonal pattern in this species.

Extreme summer temperatures can render shallow reef habitats inhospitable to large roving herbivores. This has the potential to provide macroalgae temporal refuge from grazing. The large bodied TPs are more prone to the negative effects of extreme high temperatures compared to small individuals. This implies that, global warming will primarily affect larger species or size-classes and will result in communities that are composed of smaller species and individuals. Enclosed seas such as the Red Sea already are experiencing extreme high temperatures. Fish populations from these areas will be more prone to rapid alterations. If this happens, grazing impact by parrotfishes will be greatly reduced since the large classes are the major contributors to grazing. Rises in habitat temperature will also alter life history traits of protogynous species. Mortality rate of males will be higher than that of females owing to their larger size. This will result in earlier size and age at sex change and prevalence of older none-sex changing females.

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Summary

This thesis investigates the effects of strong seasonality on grazing on a coral reef in the southern Red Sea, an area known for its monsoon driven seasonality in rain fall, irradiance and extreme summer temperatures. These environmental conditions drive significant seasonal changes in the biomass, distribution and composition of benthic algal communities.

Habitat use patterns of different herbivorous fish species were investigated. One abundant coral reef grazer – the rusty parrotfish *Scarus ferrugineus* – was selected as a focal species. This species is a sequential protogynous hermaphrodite. Individuals generally change from an initial female phase to a terminal male phase. Feeding ecology, growth, demography and reproduction of *S. ferrugineus* were studied in detail.

At the study site near Sheikh Said Island (Massawa, Eritrea), we recorded 18 roving herbivorous fish species, in numbers and biomass dominated by parrotfishes. Bi-monthly monitoring revealed that during most of the year, roving herbivores aggregate in the shallow reef zones but are not evenly distributed over these zones. The abundance at the deep fore reef is low throughout the year. Habitat use patterns correspond to the availability of preferred food. Browsers are common on the macroalgae dominated reef flats. Scrapers dominate the reef crest; a zone that is characterized by high cover of algal turfs. In summer, the distinct community structures among reef zones are lost as reef flat herbivores tend to exploit deeper reef zones and some reef crest species venture on to the reef flat. This seasonal change in habitat use is attributed to the extreme water temperatures (reaching 36°C) and to the lack of food and shelter on the reef flat.

Scarus ferrugineus represents ~34% of the total roving herbivore biomass. It's foraging is highly selective primarily targeting dead coral substrates covered by turf algae. Terminal phase and initial phase individuals have the same feeding preference. Other potential food sources that are dominant during the cool season, like macroalgae and crustose corallines, are not utilized. The diurnal bite rate pattern of *S. ferrugineus* shows low bite rates in the morning and peak levels in the afternoon, similar to other reef herbivores. Feeding preferences also reveal a diurnal pattern. In the morning more bites off vertical surfaces and overhangs are taken targeting less preferred items such as crustose corallines, while in the afternoon almost all bites are on horizontal surfaces targeting turfs growing on endolithic algae. During the warmer parts of the year more bites are taken than during the cool season. As a result the total daily food intake is lowest in the cool season and highest in the May – June period. In territorial males engaged in reproductive activities, the daily intake decreases by ~23%. The relationship between temperature and bite rate in large males is parabolic while that of the initial phase fish is linear. This suggests that in summer the larger bodied males operate close to their upper temperature limit.

Growth rates were recorded using mark-recapture techniques to investigate the affect of the seasonally changing food intake. In addition, five males and five females were sampled monthly to assess body condition, measure liver mass and gonad weight and to determine the age by reading annual growth rings in otoliths. Growth in *S. ferrugineus* was highly seasonal and correlated with feeding intensity and availability of preferred food sources. Peak growth was achieved during the warmer parts of the year, while during the cool season growth ceases. Temporal changes in body condition correlate with the trends in growth. Fish in the warmer parts of the year have the highest liver and body condition, and low liver mass and body condition during the cool season. Interestingly, the reproductive activity of *S. ferrugineus* is highest during the cool season. The gonads are larger and the spawning intensity is more intense. It is argued that this species stores energy during the warmer parts of the year, which it uses to produce gametes during the cool season. The time conflict between feeding and reproductive activity may explain why reproduction is deferred to the cool season. Reproductive activity takes time which could have been spent on feeding. Thus by focusing on feeding during warmer seasons when its preferred food is abundant, the species avoids the conflict between feeding and reproduction.

The initial and terminal life phases of *S. ferrugineus* differ in body colour and size; the males are larger and more colourful. The sexual size difference between males and females is caused by a growth spurt during sex change. This surge in growth continues even after sex change is completed, which finally leads to males being ~40% larger. The majority of the terminal phase males are sex-changed from an initial female phase. About 5% of the initial phases are males. These initial phase males develop into terminal males without going through a functional female phase. The terminal phase males of *S. ferrugineus* suffer higher mortalities than initial phase females. Predation and high temperature related stress are likely factors that cause the high mortality in males.

In protogynous hermaphrodites sex change happens if an individual's expected reproductive success (ERS) increases after sex change. The ERS is a function of mortality, growth and size-fecundity skews. In *S. ferrugineus*, 4 years is the threshold age beyond which sex change is not beneficial. In this case a female reaching 4 years and beyond will not gain in fitness by changing to a male since the high male mortality will discount its fitness. Several females in the studied population crossed this threshold age and are expected to remain females for life.

Samenvatting

Dit proefschrift onderzoekt de effecten van sterke seizoenswisselingen op de begrazing van een koraalrif in de zuidelijke Rode Zee. Dit gebied staat bekend vanwege de moesson gedreven seizoensverschillen in regenval en instraling en de extreem hoge zomertemperaturen. Die milieuomstandigheden veroorzaken significante seizoensveranderingen in de biomassa, verspreiding en samenstelling van benthische algengemeenschappen.

Patronen in het habitat gebruik van diverse herbivore vissen zijn onderzocht. Een veel voorkomende grazer – de roestnekpapegaaivis *Scarus ferrugineus* – is geselecteerd als de soort waarop de aandacht is geconcentreerd. Deze soort is sequentieel protogyn hermafrodiet. Individuen doorlopen meestal een initiële vrouwelijke en een terminale mannelijke fase. De voedselecologie, de groei, de demografie en de reproductie van *S. ferrugineus* zijn in detail bestudeerd.

In het onderzoeksgebied bij Sheikh Said Island (Massawa, Eritrea), zijn 18 rondzwervende herbivore vissoorten geregistreerd, gedomineerd in aantallen en biomassa door papegaaivissen. Tellingen om de twee maanden lieten zien dat die zwervende herbivoren zich het grootste deel van het jaar in de ondiepe rifzones ophouden, maar ook dat ze niet gelijk verdeeld zijn over de verschillende zones. Dichtheden op het diepe voorrif zijn het hele jaar laag. De patronen in het habitat gebruik corresponderen met de aanwezigheid van het voorkeursvoedsel. Browsers zijn algemeen op de door macroalgen gedomineerde ondiepe rifvlakten. Schrapers domineren de rifkam, een zone die gekarakteriseerd wordt door een hoge dichtheid aan turfalgen. Tijdens de zomer verdwijnen de onderscheiden gemeenschapsstructuren doordat de herbivoren van de ondiepe rifvlaktes diepere zones gaan exploiteren en sommige soorten zich verplaatsen van de rifkam naar de vlakkere delen. De seizoensverandering in habitat gebruik wordt waarschijnlijk veroorzaakt door extreem hoge water temperaturen (tot 36 °C) en door het gebrek aan voedsel en schuilplaatsen op de ondiepe rifvlakten.

Scarus ferrugineus vertegenwoordigt ~34% van de totale biomassa van de rondzwervende herbivoren. De soort foerageert heel selectief en graast voornamelijk op dood koraal begroeid met turf algen. Individuen in de initiële en de terminale fase hebben dezelfde voedselvoorkeur. Andere potentiële voedselbronnen die dominant aanwezig zijn tijdens het koele seizoen zoals macroalgen en korstvormige kalkroodwieren worden niet benut.

Het dagelijkse hapfrequentiepatroon van *S. ferrugineus* laat, net als bij andere rif herbivoren, lage frequenties zien in de morgen en hoge in de middag. Ook voedselvoorkeur vertoont een dagelijks patroon. ’s Morgens worden er meer hapjes genomen van verticale en overhangende oppervlakten waarbij ook minder gewaardeerd voedsel zoals kalkroodwieren wordt gepakt, terwijl ’s middags bijna alle happen genomen worden van horizontale oppervlakken. Die happen bestaan uit turfjes algen met de endolithische algen waarop ze groeien. Tijdens de warme perioden van het jaar nemen de vissen meer happen dan tijdens het koele seizoen met als resultaat dat de totale dagelijkse voedselopname het laagst is tijdens het koude seizoen en het hoogst in de maanden mei en juni. Bij territoriale mannen die voortplantingsactiviteit vertonen neemt de dagelijkse voedselopname met ~23% af. Bij initiële vissen is het verband tussen temperatuur en hapfrequentie lineair terwijl dat van terminale mannen parabolisch verloopt. Dit suggereert dat de grotere mannen in de zomer tegen hun hoge temperatuur limiet aan opereren.

Groeisnelheden zijn gemeten bij gemerkte en teruggevangen vissen om het effect van de siezoensvariatie in voedselopname te onderzoeken. Daarnaast zijn maandelijks 5 mannen en 5 vrouwen bemonsterd om de lichaamsconditie vast te stellen. Daarbij zijn de massa van de lever en het gonadengewicht gemeten en is de leeftijd bepaald door de jaarringen in gehoorbeentjes (otolithen) te lezen. De groei van *S. ferrugineus* blijkt sterk afhankelijk te zijn van de seizoenen en gecorreleerd met het niveau van de voedselopname en met de beschikbaarheid van de meest gewaardeerde voedselbronnen. De groei is het sterkst tijdens de warmste perioden van het jaar en stopt tijdens het koude seizoen. Veranderingen in de conditie correleren met de trends in de groei. De beste conditie en de zwaarste levers zijn aangetroffen tijdens de warme perioden. Het koude seizoen laat tegenovergestelde effecten zien. Het is interessant om vast te stellen dat de voortplantingsactiviteit van *S. ferrugineus* het hoogst is in het koude seizoen: de gonaden zijn dan groter en de paaifrequentie is hoger. We stellen vast dat deze soort energie opslaat tijdens de warmste delen van het jaar om die te gebruiken om gameten te produceren in de koele periode. Paaien kost tijd die gebruikt had kunnen worden voor voedselopname. Het conflict tussen de tijd nodig voor voedselopname en die voor het paaien kan verklaren waarom de voortplanting vooral in het koude seizoen plaatsvindt. Door de meeste tijd te besteden aan voedselopname tijdens de warme periode wanneer het voorkeursvoedsel in ruime mate voorhanden is, vermijdt deze soort dit mogelijke conflict.

De initiële en terminale fasen van *S. ferrugineus* verschillen in kleurpatroon en grootte; de mannen zijn groter en kleurrijker. Het verschil in grootte tussen de seksen wordt veroorzaakt door een groeispurt tijdens de sekseverandering. Deze versnelling in de groei zet nog door nadat de sekse verandering is voltooid waardoor de mannen uiteindelijk ~40% groter zijn. De overgrote meerderheid van de mannen in de terminale fase zijn functionele vrouwtjes geweest tijdens de initiële fase en hebben een sekse verandering ondergaan. Ongeveer 5% van de vissen in de initiële fase zijn mannetjes. Deze ontwikkelen zich tot terminale mannen zonder een functionele vrouwelijke fase te doorlopen. De sterfte onder *S. ferrugineus* in de terminale fase is groter dan die onder de vrouwelijke vissen in de initiële fase. Predatie en stress die te maken heeft met hoge temperaturen zijn mogelijke factoren die deze hoge sterfte bij mannen kunnen verklaren.

De verwachting is dat protogyne hermaphrodieten veranderen van sekse als het reproductieve succes van een individu groter wordt na de sekse verandering. Dat verwachte reproductieve succes is een functie van de sterfte, de groei en niet lineaire relaties tussen grootte en vruchtbaarheid. Bij *S. ferrugineus* is 4 jaar de drempelleeftijd waarna sekse verandering niet meer loont om het reproductieve succes te vergroten. Bij vrouwtjes die meer dan 4 jaar oud worden zal de fitness niet toenemen wanneer ze van sekse veranderen omdat de verhoogde mortaliteit als man dat verhinderd. Verschillende vrouwtjes in de bestudeerde populatie zijn die drempelleeftijd gepasseerd en zullen waarschijnlijk de rest van hun leven vrouw blijven.

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እዚ ኣብዚ መጽሓፍ ተዘርዚሩ ዘሎ ጸብጻብ ኣብ ከባቢ ባጽዕ ካብ 2005 ክሳብ 2008 ዝተገብረ ስነፍልጥታዊ ምርምር ብዛዕባ ጽልዋ ወቕታዊ ምልውዋጥ ኩንታት ባሕሪ ኣብ መነባብሮ ኣብ ኮራል-ሪፍ ዝርከቡ ዓሳታት ብፍላይ ኣብ ሓሪድ[1] ዘተኮር'ዩ። ኮራል-ሪፍ (coral reef) ኣብ ገምገም ባሕሪ ኣብ ቀረባ ዕምቆት ብዝነብሩ ኮራልን (coral) ሰበባ ባሕሪን (Algae) ዝብሀሉ ፍጡራት ዝትሃንጸ ተፈጥሮኣዊ ሰፈር'ዩ። ሙቐት ባሕሪ ትሕቲ 18 °C ኣብ ዘይወርደሉ ትሮፒካዊ ኣከባቢ ጥራይ እዮም ዝርከቡ። ብተወሳኺ ናይ ጸሓይ ብርሃን ንኮራል ኣዝዩ ኣገዳሲ ስለዝኾነ ካብ 0-50 ሜትሮ ዕምቆት እዮም ብብዝሒ ዝርከቡ። ኣብ ጽቡቕ ኩነታት ዘሎ ኮራል-ሪፍ ብዙሕ ኮራል ከምኡዊን ድሩዓት ዓይነት ሰበባ (corraline algae) ይህልዎ። ኣብዚ ግዜ'ዚ ብሰንኪ ደቂ ሰባት ዝገብሩዎ ምትእትታው ብዝሒ ኮራል ኣብ ብዙሕ ክፋላት ዓለም እንዳጎደለ ይኸይድ ኣሎ። እብ ክንዲ ኮራል ድማ ዓበይቲ ሰበባ ባሕሪ ይስስኑ። እዚ ምምዝባል ወይ ምንካይ ብዝሒ ኮራል ኣብ ህይወታዊ ብዙሕነት ብፍላይ ድማ ኣብ ዓሳ ኣሉታዊ ጽልዋ ኣሎዎ።

ካብቶም ብዙሓት ምምዝባል ከምጽኡ ዝኽእሉ ባእታታት እቶም ቐንዲ እዞም ዝስዕቡ ይርከብዎም፥ 1) ብምብሕጓግ መሬት ሐመድ ብብዝሒ ናብ ኮራል-ሪፍ ምስዝኣቱ፣ 2) ብሰንኪ ብከላ ዓቐን ንጥረ ነገራት ከም ናይትሬትን ፎስፌትን ካብ መጠን ንላዕሊ ምስዝውስኽ፣ 3) ካብ ቅጥዒ ዝሐለፈ ምግፋፍ ዓሳ፣ 4) ምቅይያር ክሊማ ብፍላይ ደቂሰባት ዘምጽእዎ ምውሳኽ ሙቐት ዓለም። እቲ ብብዝሒ ዝረኣይ ዓይነት ምምዝባል ፤ ኮራል ብዓበይቲ ሰበባ ባሕሪ ክዕብለል ከሎ'ዩ። ሰበባ ዝምገቡ ዓይነት ዓሳ ነዚ ምምዝባል ንኽይመጽእ ዓቢ ተራ እዮም ዚጻወቱ። እዞም ዓሳ ብብዝሒ እንተሃሊዮም ነቲ ሰበባ ስለዝቆጻጸርዎ ኮራል ንኽዓቢ ዕድል ይረክብ። ስለዚ ህላዌ እዞም ዓሳ ንጥዕና ኮራል-ሪፍ ኣዚዩ ኣገዳሲ'ዩ።

ደቡባዊ ቀይሕ ባሕሪ ምስ ካልኦት ከባቢታት ክወዳድር ከሎ ብዙሕ ብደቂሰባት ኣይተጸልወን። ብፍላይ ገማግም ባሕሪ ኤርትራ ኣብ ዝሓሸ ኩነታት ይርከብ። እዚ ከባቢ ቅንዲ መለለይኡ ልዑል ሙቐቱን ወቕታውነቱን እዩ። እዚ ኣብዚ ከባቢ ዝርአይ ሙቐት ንኣብ ካልእ ቦታ ዝርከቡ ኮራል ክቐትሎም ይኽእል። ኣብ ደቡባዊ ቀይሕ በሕሪ ዝርከቡ ኮራል ዓሳ ከምኡዊን ሰበባ ግና ተጻዋርነት ዘማዕበሉ እዮም። እዚ ፍሉይ ባህርያት ድማ ንስነፍልጠጣዊ ምርምር ተደላይ ስለዝኾነ ንደቡባዊ ቀይሕ ባሕሪ ኣገዳሲ ነይ መጽናዕቲ ቦታ ይገብሮ። ንኣብነት ህይወታውያን ብኸመይ ነቲ ውቕታዊ ለውጢ ከምዝሰግርዎ ወይ ነቲ ኣዚዩ ብርቱዕ ሙቐት ከምዝጻወርዎ ከተጽንዕ ትኽእል። ኣብዚ ዝተረከበ ፍልጠት ድማ ኮራል-ሪፍ እንታይ ዓይነት ለውጢ ከጋጥሞም ከምዝኽእል ንምግማት የኽእለካ። ንኣብነት ምስምቕያር ክሊማ ብፍላይ ድማ ምስምውሳኽ ሙቐት ዓለም ክመጽእ ዝኽእል ለውጢ። እዚ ድማ ንውሕሉል ምምሕዳር ተፈጥሮኣዊ ጸጋታት ሐጋዚዩ።

እዚ ሪፖርት'ዚ ኣቶኩሩኡ ኣብ በላዕቲ ሰበባ ዝኾኑ ዓሳ ኮይኑ ብኸመይ ኣገባብ ነዚ ፍሉይ ባህርያት ናይዚ ከባቢ ክምዝብድህዎ ንምፍላጥ ዝተገብረ መጽናዕቲ'ዩ። ካብቲ ዝተጸንዐ ነጥብታት፥ 1) ክንደይ ዓይነት በላዕቲ ሰበባ ዝኾኑ ዓሳ ኣለዉ ኣበይ ቦታኸ ይርከቡ 2) ወቕታዊ ምብዛሕን ምጉዳልን ሰበባ ንኣመጋግባ ናይ ሓሪድ (*Scarus ferrugineus*) ይጸልዎዶ? 3) ኣብ ዕብየትን ምርባሕን (ምጽፋይን) ከመይ ዓይነት ጽልዋ ኣለዎ 4) ዕድመን (መዋእል) ፣ ምጣነ-ሞትን ሓሪድ ከመይ ይመስል።

ገማግም ባሕሪ ኤርትራ ልዑል ወቕታዊ ምቅይያራት ከምዘርእይ ኣተውብርሃንን ዘካርያን (Zekeria, 2003; Ateweberhan, 2004) ቅድሚ ሕጂ ኣብ ዝገበርዎ መጽናዕቲ ዘጊቦሞ'ዮም። ኣብዚ ናይ ሕጂ ዝተገብረ ምጽናዕቲውን ተመሳሳሊ ትዕዝብቲ ተጌሩ። ብሰንኪ ኣዚዩ ብርቱዕ ሙቐት ክረምቲ ፣ ዓበይቲ ሰበባ ባሕሪ ይጠፍኡ ኣብ ክንድኦም ደቀቕቲ ፣ 0-2 ሚሊሜትር ዝቑመቶም ሰበባ (turf algae) ይበዝሑ። ኣብ ግዜ ቑሪ (ታሕሳስ - ምያዝያ) እቶም ዓበይቲ ይምለሱ ብዝሖም ይውስኽ ፣ ቀልጢፎም'ውን ይዓብዩ። እቲ

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[1] ሓሪድ (ብዓረብኛ) ብእንግሊዘኛ (parrotfish) ካብቶም ኣብ ኮራል ብብዝሒ ዝርከቡ ዓይነት ዓሳ'ዮም። ኣብ ዓለም ኣስታት 90 ፣ ኣብ ቀይሕ ባሕሪ ድማ ኣስታት 18 ዝተፈላለዩ ዘርኢ ኣለዉ። ኣብቀይሕ ባሕሪ ብፍላይ አብ ደቡባዊ ክፋሉ እቲ ብብዝሒ ዝርከብ ዘርኢ *Scarus ferrugineus* ይብሃል።

ዝበዝሐ ወቕታዊ ለውጢ ኣብቲ ኣብ ቀረባ ዕምቖት (0-1 ሜትር) እዩ ዝርአ። ብዘይካ እዚ ወቕታዊ ለውጢታት ፤ ሰበባ በሕሪ ዝርጋሐኦም'ውን ይፈላለ'ዩ። ዓበይቲ ሰበባ ኣብቲ ቀረባ ክኾኑ ከለዉ እቶም ደቀቕቲ ድማ ኣብ ዕሙቕ ዝበለ ይርከቡ። ተመሳሳሊ ናይ ዝርግሓ ፍልልይ ኣብቶም ዓሳውን ይርአይ። ክምኒ ሰጃን[2] (*Siganus rivulatus*)፣ ሓሪድን (*Hipposcarus harid* ዝብሃል ዘርኢ) ፣ ጁነሕ[3] (*Acanthurus gahhm*) ኣብቲ ቀረባ ዕምቖት ይርከቡ። ካብዚ ቁሩብ ዕሙቕ (1-3 ሜትር) ኢሎም ድማ ክምኒ ዘርኢ ሓሪድ (*Scarus ferrugineus*) ን (*Chlorurus sordidus*) ይዕብልሉ። ኣብቲ ዓምዩቕ (3-10 ሜትር) ክፋል ናይ ኮራል-ሪፍ በላዕቲ ሰበባ ኣዚዮም ዉሑዳት እዮም። እዚ ዝተጠቕሰ ዝርግሐ ኣብ እዋን ክረምቲ ሙቐት ምስጀመረ ይልወጥ ፤ ማለት እቶም ዝበዝሑ ዓሳ ናብቲ ማእከለይ ዕምቆት ይውሕዙ። እዚ ዝኾነሉ ምኽንያት ድማ እቲ ቀረባ ክፋል ልዑል ሙቐት ስለዝህልዎን መግቢ (ሰበባ) ስለዝጎድልን'ዩ። ኣብ ከባቢ ባጽዕ ብሓፈሻኡ ኣስታት 18 ዝተፈላለዩ ዘርኢ ተመገብቲ ሰበባ ዝኾኑ ዓሳ መዝጊብና። ሓሪድ ዝብሃሉ ዓሳ ብቁጽሪ ከምኡዊን ብሚዛን (ብዝሒ/ኪሎግራም ኣብ ሐደ ሄክታር) እቶም ዝበዝሑ ዓይነት እዮም።

ሓደ ዘርኢ ሓሪድ (*Scarus ferrugineus*) ኣስታት 34% ብሚዛን ናይ ተመገብቲ ሰበባ ይውክል። እዚ ዝስዕብ ጽብጻብ ነዚ ዘርኢ ሓሪድ ጥረይ ይምልከት። ሓሪድ ኣብቶም ኣብ ዝሞተ ኮራል ጠቢቖም ዝቦቕሉ ንኣሽቱ ሰበባ እዩ ዝምገብ። ኣብ ግዜ ዛሕሊ ብዝሒ ነይዚኦም ንኣሽቱ ሰበባ ስለዝጎድል ካልኦት ዓይነት ሰበባ ማለት ድሩዓት ሰበባ (coralline algae) ሐዊሶም ይምገቡ። ኣብ ግዜ ሙቐት ግን ደቀቕቲ ሰበባ ብብዝሒ ስለዝርከቡ ዳርጋ ሙሉእ ብሙሉእ ኣብኦም ይምገቡ። ኣብ ሓደ ምዓልቲውን ኣመጋግብኦም ተመሳሳሊ ለውጢ የርኢ። ኣብ ስዓታት ንግሆ ቀስ ኢሎም ይምገቡ ብብዝሒ ድማ ኣብ ትኹል (vertical) ወይ ኣብ ዝተንጠልጠለ (overhangs) ጽፍሒታት ኣቶኪሮም ይምገቡ። ከም ውጽኢቱ ብዙሕ ዝተደርዓ ሰበባ ይምገቡ። ካብ ፊርቂ መዓልቲ ንድሕሪት ግና ኣብ ጋድም ጽፍሕታት ኣብቶም ንኣሽቱ ሰበባ ዝርከብዎ ጥራይ ይምገቡ። ቅልጣፈ ኣመጋግብኦም (ኩላሶ ኣብ ደቒቕ) ኣብ እዋን ሙቐት ይበዝሕ ካብ ኣብእዋን ቑሪ። ከም ውጺኢቱ ኣብ ምዓልቲ ዝምገብዎ ብዝሒ (ግራም ሰበባ ንምዓልቲ) ኣብቲ ናይ ሙቐት ወቕቲ እዩ ዝበዝሐ።

ዕብየት ሓሪድ ብሽምዚ ዝስዕብ ኣገባብ ተጸኒዑ ፤ ዓሳ ብምሓዝ ሚዛኖምን ቁመቶም ዓቂንካ ፍሉይ መለለይ ምልክት ብምግባር ንባሕሪ ትመልሶም። ድሕሪ ክልተ ኣዋርሕ ከምእንደገና ዓሳ ብምግፋፍ ነቶም ምልክት ዘለዎም ክሳብ ክንደይ ሚዛን ወይ ቁመት ከምዝወሰኹ ብምዕቃን ዕብየቶም ትግምግም። ኩነታት ነብሶም ወይ ክሳብ ክንደይ ስብሒ ደሊቦም ከምዘለዉ ንምግምጋም ድማ ፣ ሐሙሽተ ኣንስትዮት ሐሙሽተ ተባዕትዮት ወርሓዊ ብምእካብ ክብደቶም ፣ ክብደት ጸላም ከብዶም ፣ ክብደት እንቋቕሖኦም ኣብ ላቦራቶሪ ትዓቒኑ።

ኣብ ግዜ ሙቐት ኩነታት ነብሲ ነይዘም ዓሳ ኣብ ዝልዓለ ጥርዙ ይበጽሕ። ንኣብነት ኣብ ጸላም ከብዶም ዝኸዝንዎ ስብሒ ዝልዓለ ሚዛኑ ኣብ ግዜ ሙቐት'ዩ ዝርአ። ብተወሳኺ ዝቐልጠፈ ዕብየት ኣብዚ ወቕቲ'ዩ ዝርአ። ብመንጽሩ ኣብ ግዜ ዛሕሊ ዕብየቶም ደው ይብል ፣ እቲ ኣብ ግዜ ሙቐት ዝኸዘንዎ ስብሒ እናተጠቀሙውን ይሓልፍዎ። ስለዚ ኣብ መወዳእታ ናይ ዛሕሊ ወቕቲ ኣካላቶም ይዓብር ፣ ሚዛን ጸላም ከብዶምውን ኣብ ዝትሓተ ደረጃ ይበጽሕ።

ሓሪድ ዓመት ሙሉእ ብውሕዱ ሓንሳብ ኣብ ምዓልቲ ይጸፍዩ። እቶም ዝገዝፉ ተባዕትዮት ኣብቲ ዕሙቕ ዝበለ ክፋል ናይቲ ኮራል-ሪፍ ሓንቲ ሕዛእቲ (6 - 15 ሜትሮ ስፍሓት ዘለዋ) ይሕዙ። ኣብ ስዓታት ንግሆ ነናብ ሕዛእቶም ብምኻድ ኣንስትዮት ክመጻ ከለዋ ብሕብሮምን ብምንቅስቃሳቶም ክስሕብወን ይፍትኑ። ኣብ ሓደ ንግሆ ሓደ ብዓል ሕዛእቲ ምስ ኣስታት 16 ኣንስትዮት ክጸፊ ይኽእል። ተባዕትዮት ብሰንኪ ኣብ ኣብ ምጽፊይን ኣብ ሕዛእቲ ምክልኻልን ዘጥፍእዎ ግዜ ኣስታት 23% ካብቲ ኣብ ምዓልቲ ክምገብዎ ዝኽእሉ ንታሕቲ ይምገቡ። ወላኳ ምጽፋይ ዓመት ምሉእ እንተኾነ እቲ ብርታዔኡ (ብዝሑ) ኣብ ግዜ ዘሕሊ ይዛይድ። ኣብዚ ወቕቲ'ዚ ቑጽሪ ተሳተፍቲ ክብ ይብል ፣ ኣብ ምጽፋይ ዘጥፍእዎ ግዜ ንውሕ ይብል ፣ ከምኡውን ዓቐንን ዕብየትን (ድሉውነት ንምጽፋይ) እንቋቕሖኦም ኣብ ዝልዓለ ጥርዙ ይበጽሕ። እዚ ክኸውን ዝኽኣለ ሓሪድ ኣብ ግዜ ሙቐት ዝኸዘንዎ ስብሒ ብግዜ ቁሪ ንምጽፋይ ስለዝጥቀሙሉ'ዩ። ምጽፊይ ብዙሕ ግዜ ስለዝወስድ ፣ ኣብቲ ብዙሕ መግቢ ዝርከቦ እዋን ኣብ ምምጋብ ብምትኳርን ናይ

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[2] ሰጃን ንእስ ኢሉ (20 ሴንቲ ሜትር) ኣብቶም ዓበይቲ ሰበባ ዝምገብ ዓሳ እዩ። ኣብ ቀይሕ ባሕሪ ብብዝሒ እዩ ዝርከብ።

[3] ጁነሕ (ብዓረብኛ) መለለይኦም ኣብጭርኦም ዝርከብ እሾኽን ፣ ንጎኒ ጽፍሕ ዝበለ ኣካላቶምን ክኸውን ከሎ ኣብ ቀይሕ ባሕሪ ብብዝሒ ይርከቡ።

ምጽፋይ ተግባራቶም ብምንካይን ንምዓልቲ ዝወስድዎ ምግቢ የብዝሕዎ። ከምውጺኢቱ ሓሪድ ኣብ እዋን ሙቐት ብዙሕ ስብሒ ኽኽዝኑ ይኽእሉ። ስለዚ ንምጽፋይ ኣብቲ መግቦም ዝውሕደሉ ወቕቲ ብምክያድ ኣብ ሞንጎ ምምጋብን ምጽፋይን ክህሉ ዝኽእል ዝይምቅዳው ይንክይዎ። እቲ ዝተጸፍየ እንቛቑሖ ንኣስታት ሓደ ወርሒ ኣብ ባሕሪ ጸንበለል እናበለ ክዓቢ ድሕሪ ምጽነሕ ናብቲ ኮራል-ሪፍ ይወርድ። ዝበዝሐ ቑጽሪ ነይዞም ንኣሽቱ ውላዳት ኣብ ግዜ መጋቢት - ግንቦት እዩ ዝርከብ። እዚ ድማ ምስቲ ናይምጽፋይ ወቕቶም ዝሰማማዕ ግዜ’ዩ።

ሓሪድ ካብ ኣንስታይ ናብ ተባዕታይ ናይምቅያር ክእለት ካብ ዘለዎም ዓይነት ዓሳታት’ዩ። ኣንስትዮትን ተባዕትዮትን ብግዝፎምን ብሕብሮምን ይፈላለዩ። ተባዕትዮት ብግዝፎም ዕብይ ይብሉ ፤ ኣከላቶም’ውን ብሕውስዋስ ናይ ቀጠልያን ሰመያዊን ብጫን ሕብርታት ዝወቀበ’ዩ። እተን ብግዝፈን ንእሽዝበላ ኣንስትዮት ግን ሕብረን ናብ ቡናዊ ዝኸደ ብጫ’ዩ። ብግዳመዊ መልክዖም ኣንስትዮት ዝመስሉ ግንከኣ ተባዕትዮት ዝኾኑ ኣስታት 5% ነይተን ኣንስትዮት ይውክሉ። ሓንቲ ኣንስተይቲ ጾታ ክትቕይርኮላ ሕብራ ይልወጥ ከምኡዊን ዕብየታ ይቕልጥፍ። እዚ ኣብ ግዜ ምልዋጥ ጾታ ዝኽሰት ምቕልጣፍ ዕብየት ፤ እቲ ቕንዲ መበገሲ ናይዚ ኣብ ሞንጎ ጾታታት ዘሎ ናይ ግዝፊ ፍልልይ’ዩ። እዚ ምቕልጣፍ ዕብየት ድሕሪ ጾታዊ ለውጢ’ውን (ማለት ድሕሪ ትባዕትዮት ምዃነን) ይቕጽል። መወዳእትኡ ትባዕትዮት ኣስታት 40% ካብ ኣንስትዮት ይገዝፉ። ዝበዝሑ ተባዕትዮት ካብ ኣንስትዮት ዝተለወጡ ክኾኑ ከለዉ ዝተረፉ ካ’ብቶም ኣንስትዮት ዝመስሉ ተባዕትዮት ዝመጹ’ዮም።

ብዘይካ ኣብ ላዕሊ ዝተጥቕሰ ፍልልያት ፣ እዞም ክልተ ጾታ ኣብ መጠነሞትን ኣብ ዕድመን ይፈላለዩ። ተባዕትዮት ልዑል መጠነ ሞት ስለዘለዎም ብገምጋም ንሸሞንተ (8) ዓመት ጥረይ ይነብሩ ፣ ኣንስትዮት ብመንጽሩ ስጋብ 10 ዓመት ይነብራ። ምኽንያት ናይዚ ፍልልይ ፤ ንተበዕትዮት ዘጥቅዑ ተጻባእቲ (predators) ወይውን እቲ ልዑል ሙቐት ደቡባዊ ቀይሕ ባሕሪ ክኸውን ይኽእል።

ናይ ኣከፋፍላ ጾታ ክልሰሓሳብ (sex allocation theory) ከምዝብሎ ፣ ኣንስትዮት ጾታ ዝልውጣ ተባዕታይ ምዃን ዝሓሸ ናይ ምጽፋይ ዕድል ዘምጽእ እንተኾይኑ’ዩ። ሓደ ዓብይ ተባዕታይ ብግዝፉ ትሓጊዙ ሕዛእቲ ክሕዝን ንኻልኦት ተበዕትዮት ከልግሶምን ስለዝኽእል ምስ ብዙሓት ኣንስትዮት ክጸፊ ዕድል አሎዎ። እዚ ስለዝኾነ ጾታ ምቕያር ብዙሓት ውሉዳት ንምግዳፍ ይሕግዝ። እንተኾነግን ተባዕትዮት ሓጺር ዕድመ ስለዘለዎም ንውሕድ ዝበለ ዓመታት’ዮም ክጸፍዩ ዝኽእሉ። ኣንስትዮት ብመንጽሩ ጾታ እንተ ዘይቀይረን ንብዝሕ ዝበለ ዓመታት ክጸፍያ ዕድል ኣለወን። ስለዚ ክልተ ትጻረርቲ ነገራት ኣሎዉ ማለት’ዩ ፤ ተብዕታይ ኮንካ ንሕጺር ግዜ ወይ ኣንስተይቲ ኮንካ ንንውሕ ዝበለ ግዜ ምርባሕ። ንእሽቶይ ዕድመ ዘለዋ ኣንስተይቲ (ንኣብነት 2 ዓመት) ጾታ እንተቐይራ ኣስታት 6 ዓመት ከም ተባዕታይ ኮይና ክትራባሕ ስለትኽእልን ፣ ብዙሐት ዉላድውን ክትገድፍ ስልትኽእልን ምቕያር የወጽኣ። በንጻሩ 4 ዓመት ወይ ካብኡ ንላዕሊ ዕድመ ዘለዋ ግን ከም ተባዕታይ ኮይና እተሕልፎ ግዜ ስለዝሓጽር ጾታ ዘይምቕያር የዋጽኣ። በዚ መሰረት ጾታ ዘይቅይራ አንስትዮት ክህልዋ ይኽእላ። ኣብቲ ዘጽናዕናዮ ሓሪድ ብዙሐት ጾታ ዘይቀየራ ኣንስትዮት ረኺብና።

ንምድምዳም ፣ ብሰንኪ ወቕታዊነት ነይ ሙቐት ከምኡዊን ምብዛሕን ምጉዳልን ሰበባ ባሕሪ፣ ሓሪድ ኣብ ኣመጋግባኦም ፣ ኣብ ዕብየቶም ፣ ኣብ ናይ ምጽፋይ ባህርያቶም ወቕታዊ ለውጥታት የርእዩ። እቲ ልዑል ሙቐት ክረምቲ ነቶም ዕብይ ዝበሉ (ብብዝሒ ተባዕትዮት ዝኾኑ) ብኣሉታዊ ይጸልዎም። ኣመጋግባኦም ከምዝንኪ ይገብሮ ፣ መጠነሞቶም ከምዝውስኽ ይገብሮ። እዚ ውጽኢት ፣ ምስ ምውሳኽ ሙቐት ዓለም ኣብ ኮራል-ሪፍ ዝነብሩ ዓሳ ፣ ናይ ግዝፊ ፣ ናይ ዕድመ ፣ ናይ መጠነ ሞት ለውጥታት ከምዘጋጥሞም ይሕብር። እዚ ስነህይወታዊ ሓበሬታ ናይ እዞም ውቑባት ዓሳ ፣ ንምምሕደሮም ወይውን ካብ ምጽናት ንክትከላኸለሎም ይሕግዝ።

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Yohannes Afeworki grew up in Asmara, Geza banda. He attended Kohaito Elementary School and then Finote Tibeb Junior High. He studied at Halai Vocational School, before enrolling in Asmara Technical School in 1991. Yohannes graduated with a diploma in electrical technology in 1994. In 1994, he enrolled in the University of Asmara, where he studied Marine Biology and Fisheries (MBF). He graduated from this programme with a BSc degree in 1999. Between 1998-2000 he worked as a graduate assistant at the MBF department. In 2000 he enrolled in the University of Groningen, The Netherlands where he received an MSc in marine biology. Between 2003 and 2006, Yohannes worked as a lecturer at the Marine Sciences department of the University of Asmara. In 2006 he was re-assigned to the College of Marine Sciences and Technology (COMSAT) which is located in Massawa. Until April 2009, yohannes worked at COMSAT as a lecturer at the Applied Marine Sciences department. Since April 2009, Yohannes has been working on his PhD thesis.